Behaviour and Endocrinology of Meerkats in Zoos

Submitted by Katy Scott
to the University of Exeter
as a thesis for the degree of
Doctor of Philosophy in Biological Sciences
in May 2014

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature:

Abstract

Zoo-based research is important both to inform management decisions on captive animals and because zoos, at their best, provide a naturalistic environment, which it is possible to manipulate, in which scientific research can be performed. Extending research to multiple zoos enables investigation into how variations between zoos impact their occupants. Comparing zoo animals to their wild conspecifics can inform management decisions, improve breeding and reintroduction programmes, educate the visiting public and allow assessment of the relevance of zoo-based research to the broader field. The impact of captivity on social animals is particularly interesting, as they cannot determine their own social environment. Meerkats (*Suricata suricatta*) are a highly social species of mongoose which have been extensively studied in the wild, and which are common in European zoos; they are therefore an ideal focal species with which to assess the impact of aspects of the zoo environment.

This thesis presents a study of the behaviour, endocrinology and morphology of meerkats in ten zoos in the UK and one zoo in Germany. The size of captive meerkats' social groups was found to influence their behaviour and faecal glucocorticoid levels (fGCs), with animals in large groups exhibiting lower fGCs, which supports an optimum group size hypothesis. Meerkats in large groups also spent less time on sentry duty, although a sentry was posted more often in zoos than in the wild, reinforcing the model of state-dependent vigilance. Captive meerkats were found to weigh much more, on average, than their wild conspecifics, with 86.7% of adults more than two standard deviations heavier than the mean weight in the wild. Meerkats in larger enclosures were heavier than those in smaller ones; their weights also correlated with climate, with zoos in cool, dry locations having lighter meerkats.

This research did not find that high levels of hormonal stress occur frequently in zoo meerkats, but obesity may pose a health threat to many individuals and its impacts should be a priority for veterinary research.

Acknowledgements

Firstly, many thanks to my supervisor Mike Cant for initiating this project, for believing in my ability to do it, and for pushing my research in new and interesting directions. Thanks to my second supervisor Andy Young who was particularly helpful in discussing endocrinology. Thanks also to the rest of the Banded Mongoose Research Team, especially Emma Vitikainen, Jenni Sanderson, Chris Mitchell and Harry Marshall who have provided invaluable advice on data and sample collection and analysis.

Thanks to the European Social Fund, DEFRA and CLES for funding this PhD, and to the Society for Endocrinology who provided the grant which enabled me to do the endocrinological analyses at the German Primate Centre in Göttingen, Germany.

Thanks to Michael Heistermann, Andrea Heistermann and Tanja Wolf for their friendliness, support and patient teaching during my visit to their lab. Thanks to Marta Manser and Inês Braga Gonçalves, who were always very helpful in our communications about captive meerkats and glitter-feeding methodologies, and to Peter Santema for providing advice on fGC analysis and the differences between hormone analysis in wild and zoo meerkats. Thanks to Hazel Nichols and Bill Amos for their help with extracting and analysing DNA from banded mongoose cheek swabs and hair and faecal samples – a piece of research I would like to follow up in the future.

Thanks to Alex Habicher, who provided help and advice throughout this project, and Yvonne Nienhaus, whose data on wild meerkats was invaluable. Thanks to James Bellamy, who collected behavioural data at Shaldon Zoo as part of his BSc project. Thanks also to Xareni Pacheco-Pacheco for collaborating on data collection in various zoos.

Thanks to Pet Bailey, Jenny Avis, Jade Bailey, James Moore, Christine Clayton and my grandad Cliff Dimmack for providing somewhere for me to stay while I visited some of the more distant zoos. Thanks also to Amy Norris and Réka Csirmaz, and Alex Ecsy, in whose houses much of this thesis was written. Thanks to Jenni McDonald, Sally Luker, Chris Coles and Dominic Henri, who have provided support as we all negotiated each step of the PhD process together. Thank you to my parents, who first inspired my love of zoology and who have supported it ever since.

Thanks to the BIAZA Research Committee who approved my research and provided a supporting letter which facilitated the project by opening many doors. Thank you to Sue Walker, particularly for the collaboration on my literature review. Finally, I am especially grateful to the research and education departments and the keepers at all the zoos which allowed me to study their animals: Newquay Zoo, Paignton Zoo, Shaldon Wildlife Park, Dartmoor Zoo, Cotswold Wildlife Park, Bristol Zoo, Longleat Safari Park and Blackpool Zoo; also to the records keepers at Chester Zoo, Cologne Zoo and the Zoological Society of London who provided data on the weights of their meerkats. Without their collaboration none of this research would have been possible.

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1 General Introduction

The zoo environment experienced by captive animals differs in many ways from the environment which their wild conspecifics inhabit, and from other forms of captivity such as laboratories and farms. Zoo animals experience little or no predation threat, and are provided with sufficient food and veterinary treatment; their group membership, enclosure size and design, and feeding routine are outside of their control; and they are regularly exposed to the presence of familiar and unfamiliar humans (Hosey, 2005). It is important to establish how the zoo environment affects captive animals both to inform management decisions to maximise welfare, and to assess to what extent zoo-based research can be extrapolated (Hosey, 2005; Hosey et al., 2009, pp. 121–127; Melfi and Hosey, 2012). This thesis documents a multi-zoo study in which I investigate how various aspects of the zoo environment affect the behaviour, morphology and endocrinology of a species of highly social mammal, the meerkat (*Suricata suricatta*).

The main aims of the research presented in this thesis were to investigate how the zoo environment influences captive animals, by comparing between different zoo groups and between zoo animals and their wild conspecifics. This research is unusual in the large number of zoo groups which were studied, and the direct comparisons with data on wild conspecifics. I looked at the influences of the captive environment on behaviour, endocrinology and morphology, and therefore this research represents an unusually wide-ranging investigation into the effects of captivity on a species.

Meerkats were chosen as a model species for a number of reasons: they are very common in zoos, so it was possible to study more groups in more locations than is usual in multi-zoo studies; they are very well studied in the wild, so there was sufficient data for zoo-wild comparisons; and they are a highly social species, and therefore how their social structures and interactions were influenced by captivity was of particular interest. The conclusions reached in

this thesis apply specifically to meerkats, but I hope that they will also be of use in demonstrating the value of zoo-wild and multi-zoo comparisons for other species, and may, in the absence of species-specific data, inform husbandry decisions for other mongooses and social species more generally.

In this introductory chapter I first give a brief history of zoological collections, and then outline how multi-zoo research and captive-wild comparisons can be used to study zoo animals, and the advantages and drawbacks of these methods. I then summarise the natural history of meerkats, and finally outline the structure of the rest of the thesis.

1.1 A Short History of Zoological Collections

Zoos, in the sense of places where wild animals are kept for show with no intention to train or domesticate them, have been in existence in some form or other for thousands of years. There is evidence of a menagerie belonging to the kings of Egypt during the 18th Dynasty (c. 1550-1292 BC), and many ancient Chinese, Assyrian and Persian rulers kept wild animals to hunt with or to be hunted, for sacrifice, or simply to admire (Anus, 1971; Baratay and Hardouin-Fugier, 2002, pp. 17–18). A British royal zoo was maintained in the Tower of London from the reign of King John (1199-1216) and was first opened to the public in the 16th Century (Barrington-Johnson, 2005, p. 14).

Private zoological collections increased in popularity during the Renaissance (Baratay and Hardouin-Fugier, 2002, pp. 19–21). Lorenzo de Medici (1449-1492) had a menagerie which included big cats, elephants and bears in Florence, Italy (Baratay and Hardouin-Fugier, 2002, p. 19); while Louis XIV of France (1638-1715) was also a keen animal collector, and included a menagerie as part of his grand transformation of the gardens at the palace of Versailles (Baratay and Hardouin-Fugier, 2002, pp. 48–52). The transfer of this collection after the French Revolution (1791) from royal hands to the *Jardin des Plants* in Paris, where the animals were exhibited to the public for explicitly

scientific purposes, is in hindsight a key turning point in the role of zoos in European society (Baratay and Hardouin-Fugier, 2002, pp. 74–75; Hosey et al., 2009, pp. 21–22).

London Zoo, in Regent's Park, was one of the earliest zoological gardens open to the public in the sense that we now recognise (Barrington-Johnson, 2005). It was set up in 1828 by a group of naturalists from the Royal Society, led by Sir Thomas Stamford Raffles, who wished to be able to observe wild animals at close quarters: the admission of the public, who would be allowed entry for a small fee, was initially proposed purely as a method of meeting the running costs and only implemented in 1847 (Baratay and Hardouin-Fugier, 2002, p. 94; Barrington-Johnson, 2005, pp. 28–29). The expansion of travel and trade around the world which took place during the 19th Century, and subsequent encounters by people from one region with the wild animals of another, provided the possibility of trading in exotic animals. This was also a period when European powers were building empires across the rest of the world, and there was a interest amongst Europeans in the flora and fauna of these new dominions (Hosey et al., 2009, pp. 20–21).

Carl Hagenbeck (1844-1913) was a key figure in the development of the zoo in the 19th Century, and is often referred to as the father of the modern zoo (Rothfels, 2002). The son of a fishmonger, he and his father developed a sideline in trading the exotic species which arrived by sea in the port of Hamburg in the 1850s; Hagenbeck both sold these animals on to collectors and displayed them himself, allowing the public to view the current occupants of his menagerie for an entrance fee (Rothfels, 2002, pp. 44–47). Through the 1860s, Carl Hagenbeck developed an unparalleled network of animal catchers and gained many clients in the zoos, menageries and circuses which were proliferating at the time (Rothfels, 2002, chap. 2). By the mid 1870s, however, a number of competitors had sprung up to Hagenbeck's animal dealership, and the prices which he could once command had begun to fall. His response was to tour his extensive and ever-varying collection around Germany, displaying panoramas of animals from a particular region in an apparently natural setting,

often alongside groups of people native to that area (Rothfels, 2002, chap. 3). In 1898 the opportunity arose for him to build his own animal park near the village of Stellingen (Rothfels, 2002, pp. 161–177). With his experience as a showman, his aim was to present to the public a panorama which displayed exotic animals as though they were in the wild, with no visible barriers between the visitors and the animals, or between the different animal species. The decorations and backdrops to each enclosure looked like the natural environment of the animal's home range. Perhaps even more importantly, he set out to demonstrate that exotic species did not need to be kept in expensive buildings with heavy-duty heating systems to survive and thrive; instead, he acclimatised all his animals to the local environment (Hediger, 1950, p. 79). Hagenbeck's new style of zoo enclosures marked the beginning of the modern zoo, and is justifiably referred to as the Hagenbeck Revolution (Rothfels, 2002, pp. 8, 199). The new enclosure designs spread across Europe, with London Zoo beginning to acclimatise its tropical animals during the first decade of the 20th Century, inspired by new exhibits at Hamburg Zoo (Barrington-Johnson, 2005, p. 92).

While Hagenbeck and many other zoological entrepreneurs developed private animal collections as a lucrative business, other zoos were being founded through public subscription or by private benefactors for the express purpose of advancing science, promoting public education, and providing an escape from the surrounding urban environment (Rothfels, 2002, p. 199). Many bridled at the suggestion that they were merely entertainment: Herbert Whitley, founder of Paignton Zoo, closed his menagerie to the public rather than pay entertainment tax on a collection he intended to be educational (Baker, 1988, pp. 51–52). The prospectus of the Zoological Society of London states that its animals would be “objects of scientific research, not of vulgar admiration.” (Hosey et al., 2009, p. 25). An early and influential curator of Paris's *Jardin des Plantes*, Frédéric Cuvier, intended it to be a centre for zoological study, performing the same role for biologists that laboratories do for chemists (Hosey et al., 2009, p. 22). However, zoo biology in the modern sense can be said to originate with Heini Hediger's work in the 1940s and 50s. Hediger, who was curator of zoos in Basel and Zürich, was the first to systematically investigate how the zoo environment

affected its inhabitants. He placed greater emphasis on the design and furnishing of enclosures, regarding them as the animals' territory, which should provide the resources to fulfil their needs (Hediger, 1955, p. 17). Hediger was also one of the first to emphasise the need to encourage biologically suitable behaviours in zoo animals (Hediger, 1950, p. 4, 1955, pp. 25, 38).

Since the late 1950s, conservation has come to play a more central role in the philosophies of many zoos (Hosey et al., 2009, pp. 33–36). Gerald Durrell's zoo, founded by the animal collector at Les Augres Manor in Jersey, was developed with the specific aim of “aid[ing] in the preservation of animal life”, with an emphasis on developing breeding colonies of endangered species at immediate threat in the wild (Durrell, 1964, pp. 11–12). In the same period William Conway at the Bronx Zoo was developing links with *in situ* conservation projects (Hosey et al., 2009, pp. 35–36). This idea of the Zoo as an “ark” to protect its inhabitants from the perils of the cruel world, can be traced back at least as far as Hagenbeck's admirers (Rothfels, 2002, p. 175), although there is little evidence that the man himself built his Animal Park with conservation, or even animal welfare, high amongst his priorities. However, it took many years before the link between zoos and conservation was firmly established, and even longer for it to become expected of well-run zoos to be active participants in conservation projects; now, however, an involvement in conservation is a legal requirement for zoos in many countries (Hosey et al., 2009, pp. 43, 65–67). The worldwide umbrella organisation for zoos, WAZA (World Association of Zoos and Aquariums), is a member of the World Conservation Union (IUCN) and has produced an extensive conservation strategy entitled “Building a Future for Wildlife” in which it sets out the role zoos should play in conservation (WAZA, 2005).

Most of today's zoos still rely largely on entrance fees from the public to fund their ongoing existence, and so entertaining their visitors remains a crucial consideration. However, for many of the large zoos in the developed world their main priorities, as described in their mission statements, are conservation, education, welfare and research (Hosey et al., 2009, pp. 43–45; Mason, 2000;

WAZA, 2005).

1.2 Multi-zoo Research

Zoo-based research is important both to provide practical advice on maximising animals' welfare and breeding success, and as a scientific undertaking, since, at their best, zoos can provide a naturalistic physical and social environment but allow for control and manipulation which would not be possible in the wild (Melfi and Hosey, 2012). A constant problem faced by zoo-based researchers, especially those studying animals which have larger resource requirements, is that sample sizes within one zoo are inevitably small, and results are difficult to extrapolate beyond the single example. Multi-zoo studies also provide an opportunity to investigate how the various factors of the captive environment, such as enclosure size and design, social group size and structure, and feeding regimes, impact the behaviour, physiology or breeding success of a species, which can inform future husbandry decisions.

Comparisons between zoo data and the equivalent information about wild conspecifics can also play a useful role in multi-zoo studies, providing a benchmark of “normality” against which the multiple zoo groups can be ranged (see chapter 2 for a discussion of zoo-wild behavioural comparisons).

For this PhD I undertook multi-zoo research on the behaviour, endocrinology and morphology of a species of social mammal which is well studied in the wild and is commonly found in captivity, the meerkat (*Suricata suricatta*). I was able to work with ten zoos in the UK and one in Germany to collect behavioural data, faecal samples and weight records which were compared to each other and to available wild data (see appendix B for details of participating zoos).

1.3 Wild-captive comparisons

A study of captive behaviour is crucial for monitoring welfare and reproductive output as well as to assess the role of zoo animals in education and research (Hosey, 2005; Redshaw and Mallinson, 1991), but the corresponding comparison to wild conspecifics has only rarely been undertaken. Comparisons between the behaviour of animals of the same species in zoos and in the wild can be used in making management decisions in zoos to improve the success of captive breeding and reintroduction programmes; to maximise welfare; to inform enclosure design and enrichment; and to aid in education and research.

1.3.1 Why comparisons are useful

Since the behaviour of captive animals first began to be studied in detail, the benchmark against which they have been measured has been their wild conspecifics. Hediger, for example, argued that "a proper appreciation and understanding of life in captivity must be based on the closest possible study of life in the free state" (Hediger, 1950, p. 4). Since these remarks, studies of animals in their 'free state' have become more numerous and frequently include information on individual behaviour over multiple generations (Clutton-Brock and Sheldon, 2010). These studies have combined with theoretical developments in behavioural ecology to greatly improve knowledge of the evolutionary causes and proximate control of animal behaviour (Krebs and Davies, 1993), and both individual and population responses to changes in social and ecological environments (Clutton-Brock and Sheldon, 2010). Surprisingly, however, explicit comparisons between zoo animals and their wild conspecifics have only rarely been undertaken. In a few cases, captive studies have made reference to pre-existing data on wild animals, but only a handful of studies have compared wild and captive behaviour as part of the same project.

Zoos may aim to promote wild-type behaviour for a number of reasons: to

increase breeding success, particularly in programmes aimed at building up populations of endangered species; to ensure that animals intended for reintroduction are able to survive in the wild; to minimise the welfare impact captivity has on their animals; to aid in public education; and to increase the validity of research. Comparison of the behaviour of captive populations to their wild counterparts has great potential to help zoos to achieve their scientific and educational goals.

Differences in the reproductive behaviour between captive and wild individuals have been recorded in many species (Farmer et al., 2011; Forthman and Ogden, 1992), and altering factors which affect this behaviour may also alter reproduction. The adoption of wild-type behaviours is even more important in the case of captive animals destined for reintroduction to their natural habitat, and assessment of their behaviour both provides information about the likelihood of successful reintroduction for particular individuals, and facilitates post-release monitoring to see whether, and how quickly, the animals successfully acclimatise, which in turn can inform future reintroduction planning (Boyd and Bandi, 2002; Forthman and Ogden, 1992; Kerridge, 2005; WAZA, 2005, sec. 2.4).

An understanding of wild behaviour can be used to assess and improve welfare in captivity. This is a critical task for any organisation keeping captive exotic species, but defining and evaluating welfare is not simple. Health, survival and longevity can act as general indicators of welfare, but may mask physiological and cognitive stresses that impact negatively upon an animal's well-being. Stereotypies, defined as “abnormal, apparently non-functional, repetitive behaviours”, are widely used as welfare indicators, and offer conspicuous evidence that animals are experiencing social or habitat conditions which deviate from those found in the wild (Laws et al., 2007; Mason, G.J., 1991). It is less clear whether other divergences from wild behaviours are detrimental. Captive animals are subject to a range of factors that might influence their behaviour, but do not necessarily indicate poor welfare *per se*. According to motivational stimulus theory, abnormal behaviour in captivity may be due to the

lack of appropriate stimuli (Dawkins, 1988); other behavioural motivational theories, such as Lorenz's psychohydraulic model (1950), suggest that certain actions are driven by an inbuilt need and animals will attempt to express some forms of behaviour even in the absence of an appropriate stimulus (Hughes and Duncan, 1988). The suppression of such behaviours may be more detrimental to an animal's welfare than the non-expression of stimulus-driven actions if the stimulus is not present (Dawkins, 1988). 'Behavioural integrity' specifically aims to replicate a wild-type behavioural repertoire as a method of maximising welfare (Würbel, 2009). Specifically, to maximise behavioural integrity it is necessary to provide the key stimuli which promote or facilitate natural behaviours. This approach has been criticised as a basis for maximising welfare, as, for example, an animal which is being chased by a predator is unlikely to have a high level of welfare; Dawkins (2008) prefers to assess welfare by asking two questions not linked to wild behaviour: "Are the animals healthy?" and "Do they have what they want?". Würbel (2009) counters that maximising animals' pleasure, as this approach implies, is not necessarily in the animals' best interests. While these varying models place different emphasis on encouraging wild-type behaviour to maximise welfare, an understanding of how the loss of particular behaviours from an animal's repertoire affect welfare requires information on the full range of behaviours observed in the wild.

One of the central roles of zoos is as educational institutions, providing information to the public on the animals they keep and the environments in which they live (Forthman and Ogden, 1992; WAZA, 2005, sec. 5), and data on wild populations can lead to better, more naturalistic exhibits. By presenting their 'living exhibits' in a way that allows the public a window into the natural environment of the species they are observing – by using plants, sounds, and climate, as well as keeping animals in naturally-structured groups – zoos can enhance their educative power. Behaviour plays a key part in this, and by allowing the public to observe the natural behaviour of a species despite its captivity, zoos fulfil their educational role. Additionally, from a scientific and educational perspective, studies of captive animals are likely to be more informative if their behaviour is as rich and varied as that of their wild

counterparts.

1.3.2 Differences between captive and wild animals

Although comparisons with wild data when assessing the behaviour of zoo animals can prove useful, there are limitations on their role. There are inherent differences between the situations of zoo and wild animals, and data collected in both situations are subject to biases which can lead to false conclusions. In addition, the experiences of wild animals often do not reach the welfare standards considered acceptable in a captive setting. The Farm Animal Welfare Council lists 'five freedoms' which can contribute to maximal welfare in captivity: freedom from hunger and thirst; freedom from discomfort; freedom from pain, injury or disease; freedom from fear and distress; and freedom to express normal behaviour (Farm Animal Welfare Council, 1992). If zoo animals were compared to their wild counterparts using the first four criteria, captive conditions would almost invariably be assessed as providing higher welfare; in the case of the fifth criterion, however, the case is not so clear. It is in respect of this last aspect of welfare that a comparison of captive behaviour against wild measurements can be most useful. However, the behaviour displayed by an animal is affected by a range of factors, both internal and external, and so judging what is 'normal' is problematic. Animals in captivity inevitably experience a different environment to that found in the wild, because of restricted space, regular presence of unfamiliar humans, and being managed (Hosey, 2005). These factors will be expected to alter behaviour, and therefore need to be taken into consideration when comparing captive and wild individuals.

It is important to consider that the wild environment can also differ greatly, both spatially and temporally, and so the experiences of two wild individuals of the same species, or indeed the same individual at different times, and consequently their resultant behaviour, can likewise vary (Appleby, 1997; Hutchins, 2006). This variation in the behaviour of animals of a particular species in the wild depending on environmental, social and individual variations,

is one drawback of using wild-type behaviour as a benchmark. Against which wild animal, and at what point in time, are zoo animals to be measured? Captive and wild populations may also behave differently because of differences in heritable genetic traits or demographic composition. Although ideally a broad range of wild situations would be considered in order to establish ranges within which behaviour is observed, this is time-consuming and often impractical (Hosey et al., 2009, pp. 121–127; Hutchins, 2006; Veasey et al., 1996a). Different methods of tracking wild animals can result in substantially different time budgets (Veasey et al., 1996b). One method of overcoming some of the problems of variation in animal behaviour is to use multiple sets of data to establish a range which can be considered normal (Melfi and Feistner, 2002; Veasey et al., 1996b), and this can reinforce findings which are based on a small sample size (Kerridge, 2005). By looking at multiple groups in different captive habitats, too, the effect of particular aspects of captivity – enclosure size, quality or feeding regime – can be examined (Chang et al., 1999).

Since the technical difficulties encountered in the field are different to those encountered in zoos, the quality of data may vary considerably between the two contexts. It is rarely possible for the same observers to collect data using the same methodology on both zoo and wild animals, even when it would be possible to apply the same methods, and this result in extra variation being introduced into the system (Hosey, 2008; Veasey et al., 1996a). However, provided that technical limitations do not systematically bias observed patterns, it should usually be possible to design a study which controls for methodological differences in order to perform like-for-like analyses, although, of course, it must also be kept in mind that virtually all ‘wild’ behaviour is, in the present day, affected to a greater or lesser degree by anthropogenic forces, thus preventing the researcher from ever observing truly natural behaviour (Hediger, 1955, p. 14).

For zoos, maximising their animals’ welfare, encouraging successful reproduction in target species, providing animals which are suitable for reintroduction programmes, educating their visitors, and allowing valid research

to be carried out are all important aims. Measuring the behaviour of captive animals against a benchmark of wild behaviour is a tool which can help zoos to achieve all of these. While this type of analysis has its limits, with the differences between the experiences of wild and zoo animals naturally resulting in different behavioural repertoires, it is these variations which can provide important information to zoo professionals and inform their management decisions. As such, behavioural comparisons with wild conspecifics can be used by zoos in their efforts to achieve these goals.

1.4 The Natural History of Meerkats

Meerkats are a very widespread species in European zoos, and this, along with the detailed understanding of meerkats in the wild which has been gained in recent years, makes them an ideal species to perform a large-scale inter-zoo study of the effects of different aspects of captivity on a highly social species. Although the conclusions of this study apply directly only to meerkats, I hope that, by demonstrating a range of different areas of research in which multi-zoo and zoo-wild comparisons can be valuable with this one model species, I can at least inform future researchers looking to perform zoo-based research on other species. The conclusions I draw may also, in the absence of more species-specific data, aid the management decisions of zoos for not only meerkat but other species of social mongoose too.

Meerkats (*Suricata suricatta*, Schreber 1776) are a social species of mongoose (Herpestidae) found in arid regions of south-western Africa, primarily in South Africa, Botswana and Namibia (Macdonald and Hoffmann, 2008). They live in groups of varying sizes, from two to fifty individuals or more, with occasional lone roving males and evicted females also observed; group size most commonly falls within the range of ten to thirty animals, although both smaller and larger groups have been observed (Clutton-Brock, Gaynor et al., 1999). The size of the group affects its likelihood to go extinct and its members' mortality rate, with meerkats in small groups more at risk (Clutton-Brock,

Gaynor et al., 1999; Clutton-Brock et al., 2001). A meerkat group in the wild usually consists of a dominant pair, who largely monopolise breeding, and helpers, which can be their offspring of many different ages, more distant relatives, or unrelated immigrants (Griffin et al., 2003). Around 80% of pups born in a group are the offspring of the dominant female, of which around 90% are fathered by the dominant male (Clutton-Brock et al., 2001, 2006; Griffin et al., 2003). Subordinate females are reproductively suppressed by the dominant female, using attacks and the threat of eviction and infanticide (Clutton-Brock et al., 2008; Young, A.J. et al., 2006, 2008). Those subordinates which become pregnant, or which are perceived by the dominant female as a threat, particularly when she is pregnant herself, are commonly evicted from the group (Young, A.J. et al., 2006). Miscarriage is high amongst evicted females, as is hormonal stress and, it is thought, death rate, but they are often allowed to return to the group once the dominant has given birth (Young, A.J. et al., 2006). Occasionally subordinate females do breed successfully, most often when the dominant female is new, when there has been high rainfall and abundant food, or when they are older or heavier (Clutton-Brock et al., 2001, 2008). Even when a subordinate has carried a litter to term, there is a high risk that the dominant female will kill the pups before they emerge from the burrow, although this is less likely if the pups are born after her own litter (Clutton-Brock et al., 2001; Young, A.J. et al., 2008). After a gestation of about 70 days, between three and seven pups are born, weighing around 25-26g at birth (Clutton-Brock et al., 2006; Doolan and Macdonald, 1997; Rettig and Divers, 1986, p. 825). Their eyes open at between 10 and 14 days old, and they begin to eat solids 23 to 30 days after birth (Rettig and Divers, 1986, p. 825). The helpers of both sexes contribute to pup care (Clutton-Brock et al., 2001). Although the dominant female is the primary lactator, allolactation by subordinate females has been observed in around 25% of litters (Clutton-Brock, MacColl et al., 1999; MacLeod et al., 2013). Babysitting is an important and costly cooperative activity in which all members of the group participate: important because litters not being babysat are much more likely to be predated or killed by neighbouring groups, and costly because the babysitter is unable to forage for food (Clutton-Brock et al., 1998, 2000). Who babysits seems to be determined by nutritional state and hormone levels, although females and subordinates contribute more than males

and dominants (Carlson, Russell et al., 2006; Clutton-Brock et al., 2006; Doolan and Macdonald, 1999; Madden and Clutton-Brock, 2011). Once they are old enough to leave the burrow, at about 29 days, meerkat pups travel with their group between sleeping dens and foraging areas (Brotherton et al., 2001), with pups being dependant on begging from older members of the group until they learn to forage for themselves (Doolan and Macdonald, 1999; Hodge et al., 2007). Members of the group respond to pup begging calls by increasing their foraging rate, and donate an average of 18% of their finds to the youngsters (Carlson, Manser et al., 2006; Clutton-Brock et al., 2001; Hodge et al., 2007). Pups learn foraging techniques from their elders, and the development of traditions continues into adulthood, as meerkats copy other members of their group independently of external cues (Thornton and Malapert, 2009; Thornton, 2008a; b).

Meerkats are generalist feeders, eating insects and their larvae, arachnids and reptiles as well as occasionally roots, berries and other vegetation (Brotherton et al., 2001), without specialising in particular food types over their lifetime (Scott, 2009). Meerkats forage individually but the group stays together and in contact with one another using foraging calls (Townsend et al., 2010). During foraging bouts, a sentry is often posted – about 56% of the time in areas of relatively high predation, but only 12% of the time in safer regions (Clutton-Brock, O'Riain et al., 1999). The sentry finds a raised position, for example on a tree branch or atop a termite mound, from which it can survey the surrounding area for potential threats (Tatalovic, 2008). The sentry gives a variety of calls to indicate its presence and to alert the other meerkats to approaching danger (Tatalovic, 2008). These vocalisations include information on the type of threat, aerial or terrestrial, whether it is moving, and its urgency or closeness (Manser, 2001). There is no evidence that the sentry is at higher risk of predation than the foragers – although it is positioned more prominently, it will also be the animal with first warning of danger, and sentry posts are commonly located near to bolt holes – but it is forgoing the opportunity to forage (Clutton-Brock, O'Riain et al., 1999). Sentry duty therefore seems to be a state-dependant behaviour, with animals which have the least need to forage, being already sated, as the

most likely sentries (Clutton-Brock, O'Riain et al., 1999). All adults in the group undertake sentry duty, but the dominant female performs it less often than other group members (Clutton-Brock, O'Riain et al., 1999).

Dominant males employ mate guarding to maximise their paternity within a group, so subordinate adult males have very little opportunity for reproduction within their group, even if they are not closely related to the adult females (Spong et al., 2008). Inbreeding is almost entirely avoided, with relatedness between breeding pairs not differing significantly from zero (Griffin et al., 2003). It is common for subordinate males, therefore, to leave the group on prospecting forays, either alone or in small bands, in which they attempt to mate with females from other groups or to take over dominance (Clutton-Brock et al., 2006; Clutton-Brock, Gaynor et al., 1999; Doolan and Macdonald, 1996; Griffin et al., 2003). Since meerkats are highly territorial and the risk of predation is higher within smaller groups, these forays are high risk, and levels of blood cortisol are unsurprisingly higher in prospecting males than those in a group (Young, A.J. and Monfort, 2009). Females rarely leave their natal group voluntarily. The emigration of animals from an established group occurs most often in larger groups, when the marginal value of an extra member has fallen below the additional costs (Clutton-Brock et al., 2001, but see Clutton-Brock, Gaynor, et al., 1999 for contradiction). New groups can be formed by bands of emigrants. Within each group, the dominant female was usually either a founder member or inherited the role in her natal group, while a dominant male was most often either a founder or an immigrant, and thus born in a different group; dominant females maintain their role for longer than dominant males (Clutton-Brock et al., 2006; Clutton-Brock, Gaynor et al., 1999; Griffin et al., 2003). The longevity of a group is strongly correlated with the dominants' reproductive output, which can be as many as 42 offspring for males and 65 for females – an average of 2.8 litters per dominant female per year, dependant on rainfall, over a reign of up to ten years (Clutton-Brock et al., 2001, 2006; Doolan and Macdonald, 1997). Mortality in pups and juveniles is high, with about 33% of those that emerging from the burrow dying before they reach nutritional independence (Doolan and Macdonald, 1997). Thereafter, mortality is around

68% annually, with some individuals living up to five or six years (Clutton-Brock, Gaynor et al., 1999; Clutton-Brock, O'Riain et al., 1999; English et al., 2012). The major causes of death are predation and disease, although it is not unusual for pups and juveniles to be killed by members of neighbouring meerkat groups during inter-group interactions (Clutton-Brock, Gaynor et al., 1999; Young, A.J., 2003). Meerkats are highly territorial, each group defending a territory of 2 to 5km^2, and conflicts between neighbouring groups are common (Stephens et al., 2005).

Meerkats are one of the most extensively studied animal species in the wild, and provide an excellent model species for social mammals. They are classified as Least Concern by the IUCN (Macdonald and Hoffmann, 2008).

1.5 Aims of this Thesis

Meerkats have been extensively studied in the wild, and occasionally in captivity (Habicher, 2009; Hollén and Manser, 2007), but no study to date has compared multiple zoo groups with each other and with wild conspecifics to draw general conclusions about the influence of aspects of the captive environment on these highly social mammals. This thesis aims to address this absence. Multi-zoo and zoo-wild comparisons are used to analyse what aspects of the captive environment influence meerkats' behaviour, endocrinology and morphology, and to highlight for zoo professionals the situations and practices which are potentially increasing the stress their animals experience and which are detrimental to their physical health, as well as the good practices which are improving captive meerkats' welfare. This thesis deals specifically with meerkats, but by using data from an unusually large number of zoos as well as from the wild, it intends to demonstrate the advantages of using this approach in future for other species, as well as providing information which may be useful in informing the husbandry of other species of social mammals.

1.6 Structure of the Thesis

I investigated the behaviour, morphology and endocrinology of meerkats in zoos in the UK and Germany, with 147 subject animals across 11 institutions. Each chapter in this thesis is designed to stand alone, and there will therefore be some inevitable repetition in contents.

This thesis begins with an overview of the methodology used to obtain the data in the rest of the chapters, and details of the zoos and animals studied (**Chapter 2**).

In **Chapters 3 and 4**, I apply the theory of zoo-wild behavioural comparisons to captive meerkats. **Chapter 3** explores the differences in behaviour between meerkats in different social groups, to determine what aspects of their environment affect their behavioural repertoire, focussing particularly on the important social behaviours of interaction with conspecifics and performance of sentry duty. In **Chapter 4**, I investigate the effect of climate on meerkats' behaviour in zoos. The weather typically experienced in north-western Europe is fundamentally different to that of south-western Africa, and I explore how this difference affects meerkats' behaviour. The key question behind both these chapters is: in what situation does a meerkat in a zoo performs behaviour most similar to its wild conspecifics?

I then move on to the effect of various aspects of captivity on the morphology of meerkats (**Chapter 5**). Recent work establishing the patterns of growth shown by wild meerkats at the Kalahari Meerkat Project allows me to compare the weights and growth rates of meerkats in zoos to those of their wild counterparts, and I measure the prevalence of obesity in captive meerkats. I also investigate how the captive environment is linked to weight, in an attempt to establish what causes the observed divergence from wild morphology.

In **Chapter 6** I examine the physiology of captive meerkats by analysing faecal samples for glucocorticoid metabolites (fGCs), which provide an insight into the animal's hormonal stress response. I explore how fGCs are affected by aspects of the captive environment including the size of the social group and the presence and numbers of visitors. I also present a comparison between these results and the fGC levels of wild meerkats, and discuss to what extent this comparison is valid.

Finally, in **Chapter 7**, I review the results from the preceding chapters and attempt to draw conclusions about how meerkats in captivity differ from those in the wild. I make some suggestions for how this research could be useful to zoo professionals in making management and husbandry decisions, and discuss the relevance of zoo-based research in the wider scientific context.

2 General Methods

2.1 Introduction

Three different types of data were collected from the eleven institutions with which I worked which contribute to the work presented in this thesis. Eight of the zoos I visited in person and conducted scan samples to obtain data about the behaviour of the meerkats; two of these zoos contained two separate groups of meerkats which I studied, making a total of ten social groups observed. In three of these zoos (four social groups) I collected behaviour data in both the summer and the winter. In one case some of the data presented here (mainly in Chapters 3 and 4) was collected by an undergraduate student. From meerkats in the same eight zoos in which I performed behavioural observations, I collected faecal samples which were frozen and analysed to determine the concentration of glucocorticoid metabolites which they contained.

I also collected data on the weights of meerkats in captivity. In six zoos (three of those I visited to obtain behavioural and hormonal data, and three others) this data was already collected regularly as part of the animal management regime, and these zoos kindly provided the data to me. In three further zoos, this information is not usually collected but a one-off measurement was made by myself and the keepers, so that in total I had weights from meerkats in nine zoos. Details of the methodology of each form of data collection, and the participating zoos, are provided below.

2.2 Protocols for Data Collection and Sample Analysis

2.2.1 Methods to identify individual meerkats

Captive meerkats were individually identified during observations by one of three methods: in small groups, their natural distinguishing features were used; in larger groups, either hair dye or, in one case, wound spray was applied to each animal on a different part of its body, following the protocol used by the Kalahari Meerkat Project (Thornton, 2008a; b). Specifically, meerkats were tempted near the keepers with mealworms, their microchips were read, and a small dot of hair dye (Garnier Nutrisse, Liquorice 1 colour, L'Oréal, Paris, France) was applied with a paintbrush to a specific point on the body, without the need for capture. The meerkats showed no noticeable signs of awareness of the dye, which typically wore off in three to four weeks. The identifying marks were cross-referenced against the animals' microchips to compile information on life-histories. The care and conditions of the meerkats were unaffected by this study, with the aim that data would reflect the normal experiences of captive meerkats.

2.2.2 Behavioural observation technique

Behavioural data was collected by scan sampling all the meerkats in the enclosure. An ethogram was developed in January 2011 based on that used by Habicher (2009, pp. 96–100) on wild meerkats and observations of meerkats at Newquay Zoo (see appendix A). At each zoo, the enclosure was divided into between 6 and 12 different sections, mostly defined by clear physical markers (for example differences in height, changes in substrate, covered or not); of these sections, those which provided an elevated position which the meerkats could access to perform sentinel duty were identified. Data was collected by observing the meerkats from the public area, to reduce the likelihood of the observer influencing behaviour. Observations were made in 20-minute-long

sessions, with a scan sample performed every two minutes recording the location and activity of each animal, giving 11 data points for each animal in each session. Scan samples were the technique chosen primarily in order to allow direct comparison with wild data, as discussed in more detail in section 2.4.1 below. In addition, the temperature was recorded each session, and the weather, number of visitors within 2m of the enclosure perimeter, presence of large birds or aircraft and any other notable factors, such as presence of keepers or feeding, were recorded for each scan sample. A pause of at least 20 minutes was left between each session, and an average of 29.4 (range: 13 to 62) sessions were performed for each group over three to nine days. Further details on the specific situation for the meerkats in each zoo are provided below.

2.2.3 Weights

Data were collected on 110 meerkats kept in nine zoos in the UK and Germany between 2005 and 2013, with between 1 and 55 measurements of each animal (mean: 7.82 measurements). The age of meerkats at weighing varied from 12 days to 3429 days old (mean: 778.0 days). Meerkats were weighed either by tempting them onto a set of scales or when unconscious for veterinary treatment. At three of the zoos measurement was performed by the author with the assistance of zoo staff, in which case only they were only weighed once, while at the remaining zoos measurements were collected by zoo staff or other researchers and provided to the author. In most cases the group size and composition at the time of weighing was not included in the data, and therefore could not be included in models. The time of day that the animals were weighed was not consistent, and in most cases was not recorded so it was not possible to include this in modelling.

2.2.4 Faecal sample collection

In total, 140 faecal samples were collected from meerkats in 10 different social groups at eight zoos in England. In summer 2011, 48 samples, mostly of

unknown origin, were collected daily from four social groups. A further 21 samples from the same groups were collected in winter 2011/12. These samples were collected in the mornings from around the enclosure either by the keepers or the author, or opportunistically when defecation was observed during behavioural data collection sessions. In summer 2012, 40 one-off samples were collected from mostly known individuals in six social groups, using a glitter-feeding technique developed by Marta Manser and colleagues at the University of Zürich; this was repeated in winter 2012/13, with 31 samples collected from animals in five zoos. The glitter-feeding method used to identify the origin of each sample had previously been found not to be harmful in meerkats (Manser and Gonçalves, pers. comm.), but to prevent any possibility of a build-up of glitter in the animal's digestive tract it was only performed once in each six-month period. Briefly, a small quantity of food taken from the animal's daily diet – ranging from banana slices or grapes to horse meat or chicken – was coated in very fine embossing glitter. Each piece of food had a different colour of glitter on it, and each was given to a different meerkat, identified either visually or from its microchip. Food pieces were small, and used food with which the animal was familiar, to reduce the risk of the selected animal rejecting it. However, the meerkats were watched to determine in each case whether the target animal consumed its piece, and if not the food was either removed or the animal which did eat it was identified. Faecal samples were collected during the following 36 hours and the presence and colour of the glitter they contained identified on site before freezing. All samples were frozen on site immediately after collection, and were later transported to Penryn in cool boxes packed with ice. Once they had arrived they were stored in a freezer at -70ºC for between five and 87 weeks before being transferred, frozen, to the Heistermann Endocrinology Laboratory at the German Primate Centre in Göttingen.

Based on the appearance of glitter in the faeces after glitter-feeding, through-put rate in captive meerkats appears to be between 12 and 36 hours; faecal glucocorticoid metabolites would therefore represent the animal's blood cortisol levels over the previous 24 hours or so. This accords with the findings of other researchers (Manser and Gonçalves, pers. comm.).

Faecal glucocorticoid metabolite (fGC) concentrations were analysed by the author and Michael Heistermann's team at the German Primate Institute in Göttingen, Germany, using a corticosterone enzyme immunoassay, using the antibody which was established to monitor meerkat fGC by Young et al. (2003; 2006) in a radioimmunoassay. Extraction was performed following previously described methodologies (Heistermann et al., 2004). To outline the procedure: the samples were freeze dried at -20ºC, then pulverised and sieved to remove coarse material. At this stage, any obvious physical qualities of the samples were noted, such as the presence of large quantities fur or feathers in the faeces (which was thought to result from the animals having been fed chicks the previous day), or substantial amounts of sand coating the sample, due to the substrate from which the faeces were collected. As much extraneous sand was removed as possible. Between 0.0900g and 0.1100g of each sample was weighed out and the weight recorded to four decimal places. 3ml of 80% methanol was added to each sample, then they were shaken for 10min in a vortex and centrifuged at 3000rpm for 10min. 2ml of supernatant from each sample was decanted into eppendorfs for the glucocorticoid assay, and stored at -20°C until hormone analysis.

Faecal extracts were diluted 1:10 (except 3 samples with very low levels of fGCs that were diluted 1:3 and 1 sample with very high levels of fGCs that was diluted 1:100) in assay buffer (0.04M PBS, pH 7.2) and duplicate 50µl aliquots were measured by microtiterplate EIA along with 50µl aliquots of reference standard in doubling dilutions over the range of 1.9-125pg (Heistermann et al., 2006). The plates were incubated overnight at 4°C, then washed three times and incubated with 150µl streptavidin–peroxidase (HRP) for 30min in the dark at room temperature. Following a second washing step, 150µl of HRP-substrate solution was added to each well. After 45min of substrate incubation the enzyme reaction was stopped with 50µl 2M H_2SO_4 to each well. Absorbance was measured at 450nm (reference 630nm) on a plate reader. Sensitivity of the assay was 1.9pg. Specificity data (cross-reactivities) of the assay are reported in Heistermann et al. (2006). Intra-assay coefficients of variation for low and high value quality controls were 5.9% (n=16) and 7.9% (n=16), respectively.

Respective figures for inter-assay CV values were 8.1% (n=10) and 11.4%. (n=10). All fGC levels reported are expressed as ng/g dry faecal mass.

2.3 Participating Zoos

Records on the genetic origins and breeding history of meerkats in British zoos are scarce, and sometimes even the parents of an individual are not recorded. Genotyping is not performed, so the father can only be identified behaviourally, and many individuals without distinctive physical features are only identified with a high level of certainty on the rare occasions when their microchips are read, usually as part of a veterinary procedure. Meerkats are frequently moved around, and the records from the zoos I visited show that there is a high level of genetic mixing between groups. However, since meerkats are not a species of concern and do not have a dedicated captive breeding programme, the records of this are very limited. To identify the original founding wild animals from which current zoo populations descend would be a practically impossible task. This being the case, and with no detailed records or genetic analysis, it is impossible to assign a subspecies to the current captive zoo population. Insofar as there are distinct differences between wild populations, it is likely that zoo meerkats are a hybrid of these.

2.3.1 Blackpool Zoo

Blackpool Zoo is located on the eastern edge of Blackpool, a town on the Lancashire coast in the north-west of England. I visited Blackpool Zoo once during this research project, from the 8th to the 11th of August 2012. At that time there were two groups of meerkats in the zoo, one large breeding group which had just produced a new litter of pups, and a male-female pair. I collected data only on the pair, which were housed in a large enclosure shared with an aardvark. This enclosure had an outdoor area approximately 202m^2 and an indoor area about 34m^2. The outdoor area had a packed, sandy substrate that

was not suitable for digging, and also featured small hillocks, fake termite mounds, logs and branches which the animals could stand on to give them an elevated position. There was shelter in the outside area under a rock-type overhand and underneath a large bush. The outdoor area was surrounded by a wall about 160cm high, with glass panel inset in it to allow viewing. Inside there was an area visible to the public through a glass panel which contained boxes, a logpile, and different levels. There was also an indoor area out of the view of the public. The enclosure was cleaned in the mornings, and the animals were fed before the public arrived, at lunch time, and in the evening. The two meerkats were distinguished visually, as the difference between them were distinct enough not to need artificial marking.

At Blackpool Zoo I performed 24 20-minute-long scan-sample sessions over four days, at times ranging from 9:45am to 16:40pm. I also performed glitter-feeding on 10th August 2012 and collected faecal samples the following day. No weights data was collected from the Blackpool Zoo meerkats.

2.3.2 Bristol Zoo

Bristol Zoo is a long-established city zoo located in the Clifton area of Bristol in the south-west of England. I visited it twice, once, from 19th to 22nd June 2012, to collect behavioural data and faecal samples, and a second time on 12th and 13th February 2013 to collect faecal samples only. Bristol Zoo had the largest group of meerkats included in this study, with ten adults, three juveniles and four pups at the time of the scan samples. Of the adults, two were female, including the dominant female who was mother to all the subordinates, and the remaining eight were male. The subordinate adults were from four litters born between February 2009 and May 2010. The juveniles were born in February 2012 and the pups in April 2012, so the latter were approximately two months old when the study took place.

The meerkat enclosure at Bristol Zoo contained both an indoor and an outdoor

area. The outdoor area was about 54m^2, about a quarter of which was overhung by an extension to the roof of the house. The substrate was too sandy for the meerkats to dig their own tunnels, but the enclosure contained a large rock pile and a number of logs and rocks which could be used as raised look-out points, as well as a large hollow fake rock in one corner which contained perspex hemispheres which children could look through. The walls were mostly perspex, with wire fencing on the side furthest from the public. The were several large trees in the enclosure, too smooth to climb but which overshadowed most of the outdoor area. The indoor area was split into two, one half of which was in a house which the public could also access, on the other side of a glass barrier, and the other half without public access. These areas also had a sandy substrate, and contained rock piles and nesting boxes. The total indoor area was about 28m^2. At the time of behavioural observation, the meerkats were fed twice a day. In the morning they usually got 44g mice per animal or, once a week, 22g crickets or locusts. In the afternoon they were given 3g scattered live food per animal during a public talk at 2pm, and further food depending on the day of the week, as follows:

Day	Food per adult meerkat (half for juveniles)
Monday	1g carnivore pellets and 10g locusts or 6g crickets
Tuesday	30g boiled egg and 10g locusts or 6g crickets
Wednesday	Live food from morning allowance
Thursday	1g carnivore pellets, 10g locusts or 6g crickets, and 69g pear, tomato, corn and cucumber
Friday	30g boiled egg and 10g locusts or 6g crickets
Saturday	10g locusts or 6g crickets
Sunday	10g locusts or 6g crickets

The meerkats at Bristol Zoo were identified by marking their fur with hair dye, which was applied to a distinct part of their head, back or legs after confirming their transponder ID. Twenty-five 20-minute scan samples were performed over four days in June 2012, at times between 9:20am and 4:40pm. Glitter feeding was performed on 21st June 2012 and 12th February 2013, and the faecal samples were collected and frozen on 22nd June 2012 and 13th February 2013.

The meerkats at Bristol Zoo are weighed opportunistically as part of the husbandry regime, and 29 measurements were provided to me of 12 animals weighed on 11 separate occasions between March 2003 and July 2012.

2.3.3 Chester Zoo

Chester Zoo is the home of the North of England Zoological Society and is situated to the north of Chester in north-west England. Although I visited Chester Zoo several times to work with researchers there, I did not collect any behavioural data on the meerkats. I was however provided with weights data which is collected regularly as part of the husbandry regime. I was given 24 measurements of 15 different animals weighed on eight occasions between March 2011 and January 2013. During this period the composition of the group varied, with some animals leaving the zoo and pups being born. The enclosure in which the meerkats lived consists of an indoor and an outdoor area; the indoor area was about 36m^2, contained fake termite mounds and artificial burrow and tunnels, and could be viewed by the public through a glass window along one side. The outdoor area was about 176m^2 with a gritty substrate, surrounded by a high concrete wall. The animals were separated from the public by a glass fence about 1m tall. I have not been able to obtain information about the animals' diet or husbandry regime.

2.3.4 Cologne Zoo

Cologne Zoo is located within the city of Cologne (Köln) in North Rhine-Westphalia in western Germany. I was able to visit Cologne Zoo once during this study to interact with researchers based there, but I did not collect behavioural data or faecal samples. Staff at Cologne Zoo collected extensive data on the weights of their meerkats for a project in 2008, and they provided me with 265 weights of 21 animals, taken on 20 different dates between July and October 2008. The enclosure in which the meerkats are kept was built in 2003 and is described in detail in Zimmerman et al. (2004) along with their diet

and husbandry at that time, which I am told has not changed substantially since the new enclosure was initiated (Habicher, pers. comm.). It has an outdoor area of around 480m^2 and a small indoor area of 10m^2. Information on the climate in Cologne was from the World Meteorological Organization's data for Cologne (http://worldweather.wmo.int/en/home.html).

2.3.5 Cotswold Wildlife Park

Cotswold Wildlife Park (CWP) is set in the grounds of a country house a few miles south of Burford, Oxfordshire, in southern England. I visited the park to collect behavioural data and faecal samples on the meerkats between 29th May and 1st June 2012, and returned in February 2013 to collect further faecal samples.

At the time of my first visit, there were two groups of meerkats at CWP. The first was a family group consisting of ten animals at the start of the study period: a dominant pair, an adult son of the dominant female, four adult offspring of the dominant pair (two males and two females all from the same litter), and three pups just over two months old. The dominant female was heavily pregnant at the start of the study and gave birth to a litter of at least two pups on 30th May. This group lived in an oval enclosure within the walled garden area of the park, with an outdoor area of about 97m^2 and with access to an indoor area of about 4m^2, some of which was visible to the public through a pane of glass but which also contained wooden boxes in which the meerkats could be out of sight. The substrate of the outdoor area was gritty sand. There was also a rock pile which the animals could climb and a hollow tree which the meerkats could sit inside or on top of, and which was used regularly by the sentries and elevated them above the level of the public. They were fed three times daily: before the public entered the zoo, at lunchtime, and in the middle of the afternoon. The meerkats were distinguished by each being marked with red veterinary wound spray on their head, back or limbs after their ID transponders had been read. This performed the same function as the hair dye method of marking, but the staff at

CWP were happier to use wound spray as they had used it before on meerkats, and it stayed in place for the four day study period. The disadvantage of this method compared to hair dye was that members of the public sometimes mistook the red marking for blood.

The second group of meerkats at CWP consisted of three adult brothers from the same litter. The enclosure for this bachelor group was about 126m^2 and mostly filled with a large flat rock about a metre tall, with a substrate of sand around the base. There was also an indoor enclosure of around 5m^2. The outdoor area was shaded by trees for much of the day. Their feeding regime was similar to the other meerkat group. The three meerkats were identified by their physical distinctions rather than an artificial mark.

I performed 20 scan samples on the family group from 29th May to 1st June 2012, at times between 8:55am and 5:00pm. I performed 13 scan samples on the bachelor group from 30th May to 1st June during the same time frame. I collected faecal samples from both groups on 1st June 2012, having used a mixture of glitter and food colouring to mark their food the previous day. Faecal samples were also collected from the family group on 12th February 2013, using pure glitter-feeding. No weights were collected at CWP.

2.3.6 Dartmoor Zoo

Dartmoor Zoo is a small family-run zoo on the southern edge of Dartmoor in Devon in the south-west of England. It was made famous by the book “We Bought A Zoo”, written by its owner Ben Mee, which inspired the fictionalised film of the same name. I visited Dartmoor Zoo several times during the course of this research, collecting behavioural data and faecal samples between 18th and 21st May 2012. At that point there were two meerkats, an adult male imported from Shaldon Zoo and an adult female from Newquay Zoo. These two animals had not bred; on my later return to Dartmoor Zoo, the female had been replaced by another adult female and the new pair had successfully raised two

pups. Their enclosure was in front of the main restaurant and shop, and was an elongated triangle of about 38m^2 containing a small wooden house about 2m^2. There were small bushes and rock piles, and artificial tunnels into the house. The substrate of the outdoor area was the local reddish clay soil. The public could access all sides of the enclosure, although on two side the public walkway was raised above the level of the enclosure. The meerkats were fed, along with a talk from the keeper, at 11:30 am and 4:30pm each day. I have been unable to get details of the diet.

At Dartmoor Zoo I performed 25 20-minutes scan sample session over four days between 18th and 21st May 2012 and performed glitter-feeding on 20th May. During their morning cleaning of the enclosure on 21st May the keepers collected the faecal samples for me and froze them. I returned to Dartmoor Zoo on 6th June 2013 to weigh the meerkats that were then present (the original male, a new female and two pups) and obtained weights for the two adults and one of the pups.

2.3.7 Longleat Safari Park

Longleat Safari Park is based around the Longleat estate in Wiltshire in the south of England, and is well known from being the location of the BBC's TV series “Animal Park”. I visited to collect behavioural data and faecal samples from 23rd to 26th July 2012. The meerkat enclosure at Longleat was unique amongst those I visited in being a walk-though exhibit, allowing visitors to walk along a path through the enclosure which the meerkats could also access. The outdoor area of the enclosure was about 300m^2, part of which was shared with porcupines (divided off from the rest of the enclosure by a fence through which meerkats could pass but porcupines could not). Within the porcupines' area was a house about 20m^2 which contained had a viewing area for visitors. There were also indoor areas into which the meerkats were locked at night, but these were not accessible to them during the day; however there were shallow caves in the walls in which they could shelter. In the centre of the enclosure was a

large rock which the meerkats could climb. The visitors' path wound between this rock and the wall of the enclosure and was separated from the rest of the enclosure by a decorative fence about 10cm high which the meerkats could easily negotiate; there were also artificial termite mounds and a bush in the porcupines' area of the enclosure. The substrate was gritty sand, unsuitable for digging tunnels. To prevent physical interactions between the meerkats and visitors, at least one keeper was on duty at all times, sometimes standing on the path and sometimes not. Other humans were confined to the path.

The meerkat group at Longleat consisted of fourteen adults: a dominant male and female and their twelve offspring, seven females and five males. The dominant male and one of the subordinate females were small and had weak back legs, so was given supplementary food at the end of each day. I have been unable to obtain information about the precise husbandry regime for the Longleat meerkats, but at the time of studying they were fed in the morning and the evening without visitors present, and at least once a day in the presence of visitors, with a talk. Most of the animals were fed by scatter feeding, but two of the smallest animals, the dominant male and a subordinate female, were also separated out and fed extra food. The keepers were concerned that the other animals were overweight, and so they were on a reducing diet. The meerkats were marked at the beginning of the study with hair dye on their head, body or limbs, having been identified by transponder ID. There were also two adult meerkats kept off show, which I did not study but which were weighed.

I performed 25 20-minute scan sample sessions from 23rd to 26th July 2012, between 10:20am and 19:10pm. Due to the unique set-up I was able to collect faecal samples on an ad-hoc basis throughout the study, but I also performed glitter-feeding on 25th July and collected and froze the samples on 26th July. The keepers at Longleat were concerned that their animals might be overweight, and so had been collecting data on their weights which I was able to access. They provided me with 114 observations of 16 animals, taken on 10 dates between December 2010 and August 2012.

2.3.8 Newquay Zoo

Newquay Zoo is part of the Whitley Wildlife Trust, which also owns Paignton Zoo and Living Coasts in Torbay, Devon. Its director is Stewart Muir, who is currently the chairman of the EAZA Small Mammal Taxonomic Advisory Group, under the umbrella of which European zoos' meerkats are included. He is also the former owner and honorary director of Shaldon Wildlife Trust. Newquay Zoo is located on the north coast of Cornwall, at the very south-western end of the UK. I visited this zoo numerous times during my research, including to define the ethogram at the very beginning of the project, and the staff at Newquay have been very helpful and willing to give suggestions and to try new methods, such as the hair-dye marking, glitter-feeding and weighing. The summer behavioural data presented in this thesis was collected between 4th August and 12th August 2011, and the winter data between 25th January and 3rd February 2012. For the summer data, 41 20-minute scan sampling sessions were performed at times between 9:40am and 4:40pm; for the winter data, 42 20-minute sessions were performed between 9:00am and 4:40pm. Faecal samples were collected between 4th and 12th August 2011 and on 2nd March 2013. I helped the keepers to measure the weights of some of their meerkats, but this was not a regular part of husbandry so only these one-off weights were available to be used in the analysis.

During the study the Newquay Zoo meerkat group consisted of a dominant female and her adult offspring. In summer 2011, these were four males and six subordinate females; between the summer and winter data collection period, two of the females moved to another zoo to leave four males and four subordinate females. Their enclosure was roughly 250m^2 of outdoor space and a shed of about 3m^2. The enclosure was lined with concrete and wire and then filled with a substrate which was suitable for tunnel-making, so the meerkats dug their own burrows which they used during the day, although I was informed that they mostly slept in the shed at night. The enclosure was partly shaded by trees, and also included large rocks and bushes; some the walls could also be climbed part-way, providing raised locations for sentries. The bottom wall was

about 1m tall and allowed the public the best view of the animals; part of the top wall was also accessible to the public, but the two side wall were not.

At the time of this study, the meerkats at Newquay Zoo were fed three times a day (9am-10am, 12pm-1pm and 4pm-5pm). The morning meal changed daily, alternating between (for each meerkat): one chick, one large mouse, 40g mince meat, one raw whole egg, four rat pups, and ten crickets or eight hoppers. The midday meal consisted of 52.5g of fruit, 22.5g of vegetables and 10g of mealworms or crickets per animal. The exact fruit and vegetables varied, but citrus fruit were never included. In the evening the meerkats were fed 10g of mealworms or crickets each. This was based on a diet sheet provided by Durrell Wildlife Conservation Trust. Food was mainly scatter-fed, but large items were given to individuals to ensure an even distribution.

2.3.9 Paignton Zoo

Paignton Zoo Environmental Park is a large zoo in the south west of England on the eastern coast of Devon, and it is a zoo I am particularly familiar with as I worked in the research department here for a year during my BSc degree and volunteered here afterwards. It is owned by the Whitley Wildlife Trust, along with Newquay Zoo and Living Coasts. I visited Paignton Zoo to collect summer behavioural data on the meerkats between 22nd August and 9th September 2011, and then returned to collect winter behavioural data between 19th and 29th December 2011. Paignton Zoo had two groups of meerkats at that time, in adjacent enclosures, one a breeding pair and their pups, and the other a non-breeding pair. During the summer data collection period, one of the pups in the family group died, and the male was removed from the enclosure for medical treatment; he was later returned to the group. The female from the non-breeding pair died between the summer and winter data collection sessions, and the male was then moved to an off-show enclosure. I therefore only collected behavioural data on this non-breeding pair during the summer, but was able to collect faecal samples from the lone male in the winter too. The

groups were small enough that I was able to identify all the animals individually without the need for hair-dye marking, except for the case of the two pups. These were very alike and the keepers were reluctant to mark them, and one was removed part way through the summer data collection period, so I combined their observations together and made allowance for the larger amount of data by using proportions of time rather than absolute number of observations throughout the analyses.

Both enclosures were similar, with about 60m^2 of outdoor space and a small shed about 2m^2. The meerkats were also provided with heat lamps outside which were turned on during the day, and heating inside the sheds. Each enclosure had various substrates, including soil, concrete and bark chippings. The soil was suitable for digging, but any tunnels were raked over each day to prevent them developing into large tunnels which could either lead out of the enclosure or could collapse and trap the animals. There were also plants, logs and rock piles in each enclosure, and both were partly shaded by trees. Visitors could see over concrete walls about 1.2m high at the top and bottom of the enclosures.

The meerkats at Paignton Zoo are fed daily at around 8am, 12pm and 3pm. The feeding methods vary between in bowls, scatter feeding (especially with invertebrate prey), in closed cardboard boxes and in a large shallow receptacle filled with a substrate or leaves, as a form of enrichment and to encourage the animals to work for their food. Their diet varies by day of the week and availability of food, but the diet sheet specifies the following per animal:

Day	Morning	Afternoon
Monday	10g mealworms	1 small piece horsemeat
Tuesday	1 egg	10 locusts
Wednesday	100g Group C veg	1 mouse
Thursday	10g mealworms	15 snail/cockroach
Friday	100g Group C veg	10 locusts
Saturday	15 snail/cockroach	1 mouse

Sunday	100g Group C veg	10g mealworms

Analysis of the dry matter in this diet has been shown to provide 4.02kcal/g of energy, or a total of 81kcal per day; the zoo estimates that a meerkat's daily energy requirement is 114kcal/day, so this is a reducing diet (Paignton Zoo, pers. comm.).

During the summer data collection period, I performed 62 20-minute data collection sessions on both groups, at times between 9:20am and 5:40pm. During the winter I performed 45 scan sampling sessions on only the family group, between 9:00am and 4:20pm. I collected faecal samples each day during the summer behavioural data collection period, but it was not possible to identify which specific animal these came from. Samples were also collected on 23rd January 2013, and these were from known individuals using the glitter marking method. The family group was also weighed at this time. By the time these later weights and faecal samples were collected, the original female from the family group was no longer present and a new female had been introduced.

2.3.10 Shaldon Wildlife Trust

Shaldon Wildlife Trust is a small zoo in the village of Shaldon on the Teign estury on the south eastern coast of Devon, about ten miles north of Paignton Zoo. It is a compact, wooded site and the trust specialises in small mammals, particularly rodents and small primates. Behavioural data was collected at Shaldon between 31st August and 9th September 2011, and between 21st and 28th February 2012. The summer behavioural observations were carried out by James Bellamy, an undergraduate student, as part of his BSc project at the University of Exeter, and the winter data was collected by me. To maximise inter-observer reliability, before data collection started James and I discussed the ethogram in detail, and watched the meerkats for several hours, discussing their behaviour and how it would be categorised. Once we were happy with our behavioural definitions we performed scan samples independently on the same

group of animals at the same time and compared our results. We then further refined the definitions and repeated this process until we were consistently getting records that were identical over a 20 minute data collection session.

The meerkat group at Shaldon consisted of a dominant female and her six adult offspring, three male and three female, although one of these females had moved to another zoo by the time the winter data was collected. The dominant female could be recognised by a nicked ear, but the others were identified using hair dye. The enclosure consisted of about 50m^2 outdoor area, in the centre of which was a mound which contained an indoor house about 1m^2 with a heat lamp, accessed through tunnels and with glass on one side so that the public could see in. The top of the mound was a raised area used by sentries. One side of the enclosure had a glass and wood fence through which visitors could see the meerkats, visiors also had access to one other side, while the two remaining sides had tall wooden fences. The substrate was a soil and wood-chip mix unsuitable for digging tunnels. I do not have detailed information about the diets of the Shaldon meerkats.

During the summer data collection period, James performed 32 20-minute scan-sample sessions between 9:50am and 4:30pm. During the winter I performed 40 scan-sample sessions between 9:20am and 4:00pm. Faecal samples of unknown origin were collected daily during the summer behavioural data collection period. I also collected marked samples on 17th January 2013 using the faecal sampling method, and I weighed the meerkats on 23rd May 2013, although as this was not a usual part of the husbandry regime only this one set of weights was available for the analysis.

2.3.11 ZSL Regent's Park and ZSL Whipsnade

The Zoological Society of London (ZSL) owns two zoos, one in Regent's Park in central London and the other a safari park at Whipsnade in Bedfordshire. During my research I did not visit either of these sites, but ZSL regularly collect

data on the weights of their animals at both sites, and were able to send me 343 measurements of the weights of 32 animals on 134 different occasions between August 2005 and March 2013. During this period the locations and compositions of the groups in which the animals were held changed multiple times, so it was not possible to use this data for analyses involving the effects of the group composition or the enclosure.

The different groups of meerkats at ZSL are on different diets. In 2013 (when the latest weights were recorded), the group in Regent's Park Mammals North consisted of thirteen individuals which were fed 25g each of Hills Science Plan Feline Senior Light pellets, presented in a bowl and split between a morning feed at around 8:30am and an afternoon feed between 3:45pm and 5:30pm. Between 12pm and 1:30pm they were fed 20g each of mixed fruit and vegetables, chopped, dusted with a pinch of Nutrobal, and scattered around the enclosure, and 5g each of live food such as locusts, crickets or mealworms, also scatter-fed.

The second group in Regent's Park, in Animal Activities, are currently fed four times a day, and their daily diet consists of Hills 7+ Feline Light pellets, carrot, apple, sweet corn (dusted with Nutrobal) and mealworms or crickets, all of which are scattered around the enclosure. Two of the meerkats are also occasionally fed mice.

The group at Whipsnade, three animals in 2013 (when the last weights were recorded), were fed 11.3g of Hills Science Plan 7+ Feline Light pellets and 28.0g of crickets per animal per day, spread between two or three feeds and scatter-fed.

ZSL are currently trying to standardise their meerkats' diets, and to reduce the use of mealworms in order to reduce cholesterol, as they are concerned about the incidence of high cholesterol in their animals.

2.4 Sources of Wild Data

2.4.1 Kalahari Meerkat Project - Alex Habicher and Yvonne Nienhaus

The behavioural data collected in British zoos was compared to that collected at the Kalahari Meerkat Project by Yvonne Nienhaus of the University of Cologne and published in her Diploma project (Nienhaus, 2009), and by Alexandra Habicher of Cologne Zoo and the University of Cologne for her PhD thesis (Habicher, 2009). Habicher and Nienhaus collected complete diurnal time budgets of meerkats in three wild groups in the Kuruman River Reserve by scan sampling the animals once every minute for an hour at a time, between 6am and 8pm, over 12 weeks between December 2007 and February 2008. In total, 230 hours (282 hours in Nienhaus, 2009) of scan samples were collected, split evenly between the three social groups.

The three groups under observation were those named “Aztecs”, “Elveera” and “Lazuli”. There were young pups present in all three groups during the study, but only the behaviour of the juvenile and adult meerkats was recorded.

At the time of the study there were seven juvenile and adult meerkats in Aztecs, three females and four males, all the subordinates being the maternal siblings of the dominant female. The two subordinate females were born the previous February, and so were approaching a year of age; the other animals were all at least two years old.

There were eight meerkats in Elveera, two females and six males. Two of the males were the offspring of the dominant female, and one was the maternal brother of the dominant male. The two youngest, a male and a female, were born the previous January and so were about a year old; all the others were over a year old at the beginning of the study.

There were nine meerkats in Lazuli, three females and six males. All were over a year old at the start of the study. One subordinate male was the maternal brother of the dominant female; the two youngest males were the sons of one of the subordinate females.

The data collected by Nienhaus and Habicher was chosen for time budget comparisons because it provided complete coverage of the diurnal activities of wild meerkats. While vast amounts of behavioural data have been collected at the Kalahari Meerkat Project (KMP) over the years since it was founded in 1993, in most cases this is focal follows concentrating on specific behaviours (such as foraging) or specific individuals (such as dominant females), and so does not provide an overall measure against which captive behaviour can be compared. Most KMP protocols, for example, pause data collection when meerkats are underground for more than a short time. This was not the case with Nienhaus and Habicher's data, allowing me to compare a full day's activity in wild meerkats with the same in captive meerkats. Alexandra Habicher was kind enough to provide summaries of the raw data, which allowed detailed comparisons of the prevalence of different behavioural types between the wild and captive groups; I was also able to use her ethogram, so that comparisons were as reliable as possible. The behaviours recorded may not always be completely comparable between the wild and captive meerkats, for two reasons. Firstly, behaviours which are triggered by particular circumstances, either experiences such as the presence of a predator or environment such as heat lamps, cannot be expected to occur when these triggers are not present. Secondly, the behaviours that are observed my have a different purpose, such as vigilance posture which in a cold, sunny zoo environment may be used for thermoregulation. These differences in behaviour are discussed in more detail in Chapters 3 and 4.

Unfortunately, I found it impossible to observe all individuals in a zoo group when scan sampling every minute, because some zoo groups were larger than the wild ones and I was restricted to the public viewing area so could not observe from within the group, so I performed scans every two minutes rather

than every minute. I also added 20min breaks in between 20min scan sampling session, in order to maximise independence between sessions. Other than these changes, I attempted to replicate the methods used in collecting the wild data as closely as possible.

2.4.2 Other sources

All other wild data used for comparisons in this project are from published research papers or theses, referenced in the appropriate places.

2.5 Sources of Data and Methodology for Analyses

All statistical analyses in this thesis were performed either manually using excel (for chi squared and some t-tests) or, more commonly, using R 3.0.1 (R Development Core Team, 2013). Where appropriate, based on the structure of the data, classical parametric or non-parametric tests were used, but when multivariate statistics were a more appropriate choice I built generalised linear mixed models (GLMMs) which could include both fixed and random effects and in which the type of data, be it normally distributed, over-dispersed, counts or binomial data, could be taken into account by using different model types with the appropriate link function. Data simplification was performed by building a maximal model including all the terms of interest and their interactions, and then testing the removal of each top-level term to determine which had the least impact on the fit of the model. This term was then removed and the process repeated to give a stepwise approach. The minimum adequate model (MAM) was achieved when all top-level terms in the model explained a significant amount of variation. The significance of dropped terms was established by adding them to the MAM, or to the MAM plus their constituent terms if an interaction was being considered. Further details on the statistical analyses used in each chapter are included in the methods section of that chapter.

2.5.1 Chapter 3: Behaviour of Meerkats in Zoos

This chapter used the scan-sample behavioural data collected on ten groups of meerkats at eight zoos: Blackpool Zoo, Bristol Zoo, Cotswold Wildlife Park (family group and bachelor group), Dartmoor Zoo, Longleat Safari Park, Newquay Zoo, Paignton Zoo (family group and pair) and Shaldon Wildlife Trust. Only the data collected in the summer was used, to make the groups more directly comparable. Statistical analyses were carried out using the proportion of scans during which each animal was recorded as performing each behaviour – both as a proportion of all scans, and as a proportion only of those when the individual was outdoors and visible. The wild data against which this captive data was compared came from the study of Alex Habicher and Yvonne Nienhaus which is detailed above and published in Nienhaus (2009). Full details of the statistical protocols used are provided in section 3.3.3.

2.5.2 Chapter 4: Seasonal Differences in the Behaviour of Meerkats in Zoos

This chapter used only the behavioural data collected on meerkats in three groups in three zoos: Newquay Zoo, Paignton Zoo (family group only) and Shaldon Wildlife Trust. The weather was recorded at each 2min scan-sample and grouped into Rain, Cloud or Sun. While temperatures were also recorded during the data collection sessions, concerns about unreliability of thermometers lead me to decide to use data from local weather stations via the Met Office (www.metoffice.gov.uk) in the analysis of the influence of temperature on behaviour. The wild behaviour against which this was compared was from the same study as for the previous chapter, but using figures published in Habicher (2009). This wild data was collected between December and February, the Kalahari summer. Further details of statistical procedures are provided in section 4.3.

2.5.3 Chapter 5: Obesity in Zoo Meerkats

This chapter used the weights of meerkats in nine zoos in the UK and Germany, some of which were collected by me but most of which were collected as part of normal husbandry routines. The zoos from which data was collected were Bristol Zoo, Chester Zoo, Cologne Zoo, Longleat Safari Park, Newquay Zoo, Paignton Zoo, Shaldon Wildlife Trust and the two ZSL sites. The meerkats at Dartmoor Zoo were also weighed, but the number of measurements was too small to include them in analyses which break down the data by individual zoos. The wild weights which were used for comparison were those quoted in Clutton-Brock et al. (1999) and the model developed in English et al. (2012).

Further analysis of the impact of activity, enclosure size and sex on weight were performed on the data from 32 of the 110 animals included in the initial analysis, which were those for which behavioural data was available. These were the meerkats at Bristol Zoo, Dartmoor Zoo, Longleat Safari Park, Newquay Zoo, Paignton Zoo and Shaldon Wildlife Trust. An additional analysis to determine whether enclosure size, group size and the presence of pups were correlated included all the zoo groups for which I had the necessary data, which were Blackpool Zoo, Bristol Zoo, Chester Zoo, Cotswold Wildlife Park (family group and bachelor group), Dartmoor Zoo, Longleat Safari Park, Newquay Zoo, Paignton Zoo (family group and pair) and Shaldon Wildlife Trust.

Climate data were from the World Meteorological Organization's data for the nearest large city (http://worldweather.wmo.int/en/home.html). These cities were Bristol for Bristol Zoo and Longleat Safari Park, Liverpool for Chester Zoo, Cologne for Cologne Zoo, Truro for Newquay Zoo, Exeter for Paignton Zoo and Shaldon Wildlife Trust, and London for ZSL. For further details on the analyses, please see section 5.3.

2.5.4 Chapter 6: Hormonal Stress in Zoo Meerkats

This chapter uses the glucocorticoid levels (fGCs) measured from 140 meerkat faecal samples. These samples came from meerkats in ten different groups in eight zoos: Blackpool Zoo, Bristol Zoo, Cotswold Wildlife Park (family group and bachelor group), Dartmoor Zoo, Longleat Safari Park, Newquay Zoo, Paignton Zoo (family group and pair) and Shaldon Wildlife Trust. These samples can be divided into those from a known animal (59 samples), and those from a known group but unknown animal (81 samples). The 59 samples from known individuals were used to analyse whether fGCs varied with the individual-level factors sex, age and dominance. All 140 samples were included in the analysis of whether fGCs varied with the group-level factors group size, enclosure size, population density, season and presence of pups, and the condition of the sample. For 94 of the 140 samples the number of visitors present the day of the sample collection and the day before was known, and only these 94 sample were used in analysing whether fGCs varied with visitor numbers. The averages from all 140 samples were then compared to the averages found in samples from wild meerkats by Santema (2013).

3 Behaviour of Meerkats in Zoos

3.1 Abstract

The physical and social environment animals experience in captivity differs from that they would experience in the wild, and this can have effects on their behaviour. In this chapter I investigate whether meerkats, a highly social species of mongoose, behave differently in zoos to in their wild habitat, and what aspects of the captive environment influence their behaviour. I studied ten groups of meerkats in zoos and compared their time budgets to pre-existing data on the behaviour of three groups of meerkats in the wild. I found that the assumptions of independence of data points were not always met, and so investigated other statistical methods to make the analysis robust. Activity budgets varied much more between zoo groups than between wild groups, and while some zoo groups exhibited behaviour not significantly different to their wild counterparts, this similarity did not seem to be influenced by group size, enclosure size or the presence of pups. Captive meerkats, like those in the wild, spent the largest proportion of their time foraging, but spent more time active and less time in their dens than is typical in the wild. Group size affects the behaviour and survival of meerkats in the wild, and also has an effect on zoo meerkats' behaviour. Meerkats in larger groups spent less time vigilant; they were also less vigilant in the presence of more human visitors. Although the predation risk is much lower for captive meerkats than those in the wild, they have a sentry present for a larger proportion of the time; this supports the theory that sentinel behaviour is nutritionally state-dependent, although for zoo meerkats their weight was not found to be a significant predictor of contribution to sentry duty. In females, the older animals contributed more to sentry duty than the younger ones, but there was no relationship with age in males. It is important to know how the captive environment is affecting the behaviour of zoo animals because this can be used to inform management decisions to maximise animals' welfare, to advance captive breeding programmes, and to assess the wider relevance of research on zoo animals.

3.2 Introduction

The study of animal behaviour in zoos can have both direct, practical applications and more academic scientific ones. Behavioural observations can provide information on the health and well-being of captive animals and assist zoo professionals in making husbandry decisions to maximise their welfare while balancing the impacts of practical and financial considerations. Zoo are also a valuable site for the investigation of behavioural ecological questions, providing, at their best, a wild-like physical and social environment whilst still allowing experimental control (Hosey et al., 2009; Wehnelt et al., 2003). However, before either of these objectives can be achieved it is necessary to assess how the zoo environment is impacting the behaviour of the study animals (Veasey et al., 1996a; see previous chapter).

In this chapter I investigate the behaviour of meerkats in zoos (*Suricata suricatta*, Schreber 1776), and how it compares to that of their wild conspecifics. Meerkats are a highly social species of mongoose found in arid areas of south western Africa (Macdonald and Hoffmann, 2008). They typically live in groups of between ten and thirty animals, which may include both related and unrelated individuals (Clutton-Brock, Gaynor et al., 1999; Griffin et al., 2003). Breeding is largely monopolised by a dominant pair, although pup-rearing behaviours such as babysitting and pup-feeding are shared by all adults in the group (Clutton-Brock et al., 2001). Members of the social group often interact with each other, huddling together, grooming each other's fur and playfighting. These social behaviours are thought to play a role in improving group cohesion and maintaining the dominance hierarchy (Kutsukake and Clutton-Brock, 2006, 2010; Madden et al., 2009; but see Sharpe, 2005 for contradiction). Meerkats forage for food individually in a loose group, and it is common during these foraging periods for one or more members of the group to take up a raised guard position, on a vantage point above ground level, from where they scan the area for potential threats (Clutton-Brock, O'Riain et al., 1999; Tatalovic, 2008). This sentinel indicates its presence with a regular vocalisation, and uses

an alarm call to warn the rest of its group if it detects a something it perceives to be potentially dangerous (Manser, 2001; Tatalovic, 2008). The main predators of meerkats in the wild are jackals, felids, eagles and other raptors (Clutton-Brock, Gaynor et al., 1999). In the wild, the probability of the presence of a sentinel is affected by the predation risk, and each individual's contribution to sentry duty depends on its nutritional state, as well as its sex and dominance status (Clutton-Brock et al., 2002, 2003; Clutton-Brock, O'Riain et al., 1999).

The general questions which I intend to investigate in this chapter are:

1) To what extent do captive meerkats' time budgets differ from those of wild meerkats?

2) What affects captive meerkats' behaviour?

To this end, I collected data on the behaviour of ten groups of meerkats in the UK, which I compare to the behaviour of three groups of wild meerkats in the Kalahari, which were studied by Yvonne Nienhaus (2009). I look at the overall time budget of the captive meerkats, and how this compares to the wild groups. I analyse how the size of the social group affected the behaviour of the zoo groups, and then focus on sentry behaviour in zoos, investigating whether the factors which affect it in the wild also apply in captivity, and whether zoo visitors alter this behaviour.

3.2.1 Definition of terms

Sentry duty is an important cooperative behaviour which meerkats perform regularly. There are various different interpretations of the terms used in this context, so it is important to define what is meant by "sentinel", "raised guard" and "vigilance". Here, I use "vigilance" to mean any animal high sitting or high standing, the behaviour which has been referred to in the earlier sections of this

chapter, regardless of location. “Raised guarding” is an animal in an elevated position in the enclosure that is recorded as Vigilant, Stationary or Sunbathing. There is only ever one “sentinel” or “sentry” at a time: if more than one animal is raised guarding, the session is recorded as “multiple” or “all”.

3.3 Materials and Methods

3.3.1 General methods

Behavioural data was collected at eight zoos in the UK, two of which had two separate groups of meerkats that were observed: Blackpool Zoo, Bristol Zoo, Cotswold Wildlife Park (family group and bachelor group), Dartmoor Zoo, Longleat Safari Park, Newquay Zoo, Paignton Zoo (family group and pair) and Shaldon Wildlife Trust (details of the zoos and the study animals are included in appendices B and C). For three of the zoos (four groups), behavioural data was collected in summer 2011 and again in winter 2011/12; for the remaining five zoos (six groups), behavioural data was collected during summer 2012. In this chapter, I use data collected during the summer only – differences in behaviour between summer and winter are investigated in chapter 4.

Captive meerkats were individually identified during observations by one of three methods: in small groups, their natural distinguishing features were used; in larger groups, either hair dye or, in one case, wound spray was applied to each animal on a different part of its body, following the protocol used by the Kalahari Meerkat Project (Thornton, 2008a; b). Specifically, meerkats were tempted near the keepers with mealworms, their microchips were read, and a small dot of hair dye (Garnier Nutrisse, Liquorice 1 colour, L'Oréal, Paris, France) was applied with a paintbrush to a specific point on the body, without the need for capture. The meerkats showed no noticeable signs of awareness of the dye, which typically wore off in three to four weeks. The identifying marks were cross-referenced against the animals' microchips to compile information

on life-histories. The care and conditions of the meerkats were unaffected by this study, with the aim that data would reflect the normal experiences of captive meerkats.

Behavioural data was collected by scan sampling all the meerkats in the enclosure. An ethogram was developed in January 2011 based on that used by Habicher (2009, pp. 96–100) and observations of meerkats at Newquay Zoo (see appendix A). At each zoo, the enclosure was divided into between 6 and 12 different sections, mostly defined by clear physical markers (for example differences in height, changes in substrate, covered or not); of these sections, those which provided an elevated position which the meerkats could access to perform sentinel duty were identified. Data was collected by observing the meerkats from the public area, to reduce the likelihood of the observer influencing behaviour. Observations were made in 20-minute-long sessions, with a scan sample performed every two minutes recording the location and activity of each animal, giving 11 data points for each animal in each session. In addition, the temperature was recorded each session, and the weather, number of visitors within 2m of the enclosure perimeter, presence of large birds or aircraft and any other notable factors, such as presence of keepers or feeding, were recorded for each scan sample. A pause of at least 20 minutes was left between each session, and an average of 29.4 (range: 13 to 62) sessions were performed for each group over three to nine days.

For further details on each zoo and subject animal involved, see appendices B and C.

3.3.2 Independence of samples and serial correlation

There is a risk, when scan sampling every two minutes, that data points will not be randomised because the behaviour recorded is not independent of the same animal's behaviour two minutes earlier. In fact, in 44.66% of the instances when data is available, the animal is performing the same behaviour two minutes later

(9282 of 20783 records), but based on overall observed frequencies of behaviours, it would be expected that random assortment would produce repeated behaviours only 16.83% of the time. The recurrence of behaviours is higher than would be expected by chance (paired t-test, t=5.874, df=13, p<0.001). The most noticeable differences are in Huddling, where the probability of the animal still Huddling two minutes later is 49.17%, compared to a random expectation of 2.03%; Social Digging, with 25.27% repetition compared to an expected 0.92%; and Sunbathing, which is repeated 34.78% of the time after two minutes, compared to the expected 0.33%. Drinking and Keeper Interactions were never seen to be repeated two minutes later.

If observations are spread further apart through time, the data becomes less affected by the previously observed behaviour, but the problem is not altogether solved. After twenty minutes, the probability of an animal performing the same behaviour again is 25.95% (1107 of 4266 records), which is again higher than the 16.83% expected by random assortment of behaviours. This difference, across all behavioural categories, is significant (paired t-test, t=3.646, df=13, p=0.003). Again Drinking and Keeper Interactions were not seen to be repeated after a twenty minute interval, nor was Sunbathing, and Grooming occurred less than would be expected at random. Huddling, however, was still seen 22.77% of the time if it had occurred twenty minutes previously, compared to 2.03% randomly.

This temporal autocorrelation need not be a problem when constructing proportional behavioural time budgets. As long as the sampling times are representative, the high frequency of data points, while increasing correlation within the data, also provides a more accurate estimate of the time budget of the individual (Aebischer et al., 1993). The risk with this type of correlation is that the recorded occurrence of rare, long-duration behaviours is likely to be more error-prone than if a genuinely random sample of behaviours was used: Huddling, for example, is likely to either be observed on multiple consecutive occasions, representing a larger proportion of time than it actually occupies, or else will hardly be seen happening at all. For this and other interactive

behaviours, there is also non-independence between individuals, so Huddling, Allogrooming and Playfighting all require at least two participants; additionally, it might be that one animal Foraging, for example, could trigger others to copy its behaviour. Non-independence in the opposite direction is true of Vigilance, as if one animal is already acting as sentinel there is less incentive for others to perform that behaviour. For all these reasons, while the activity budgets created using the scan-sampling technique described provide a good estimate of how captive meerkats spend their time, it is misleading to treat each observation as an independent sample in statistical operations.

When comparing the time budgets in different zoos, in different wild groups, and between the zoo and the wild, as described in section 3.3.3.2 below, I faced the problem of dealing with this non-independence of samples. I used chi-squared tests to compare the groups, which use count data, with expected values of at least five in each category, and assume that each data point is independent. In this case, while I have over 20,000 data points documenting the behaviour of captive meerkats, each point is not completely independent of the others. To account for this, I calculated the results both as if there was independence, and taking a much more conservative approach by using the average number of occurrences of each behaviour over each observation session, and assuming independence only between sessions rather than between individual data points (see the results in section 3.4.1.2). The differences in results between these two methods highlight how unreliable the chi-squared method can be when independence is inaccurately assumed. Other, more complex solutions to this problem, such as using Monte Carlo Markov chains or Bayesian modelling, were not possible due to the constraints of the available data on the wild meerkats.

3.3.3 Statistical analyses

3.3.3.1 Time budgets in captivity

The total number of times each animal was observed to perform each behaviour was calculated and divided by the number of scan samples of that individual, including times when it was inside or out of sight, to give an overall proportion of time spent by the animal in each activity. For each animal, these proportions add up to one. The mean proportion of time spent on each behaviour for all animals was calculated, and the standard error of that mean.

The same calculation was performed for each behaviour, but as a proportion of the time the animal spent outside and visible. The effect of group on time spent outside and in sight was assessed by creating generalised linear models with a quasibinomial family due to overdispersion, and social group as the explanatory factor.

3.3.3.2 Comparison to wild time budgets

In 2008, data on the activity budgets of meerkat at the Kalahari Meerkat Project and in Cologne Zoo was collected by Yvonne Nienhaus and presented in her Diplomarbeit for the Universität zu Köln (Nienhaus, 2009). By collating the data I collected on ten social groups of meerkats in eight zoos in the UK into the same behavioural categories, it was possible to compare the activity budgets of these ten zoo groups with the three wild groups Nienhaus observed. The zoo behaviour included time spent inside or out of sight, as this seems to better represents the overall experience of the animal. The behavioural groups are as follows:

Nienhaus (2009) behavioural	Incorporates behaviours as defined by

description:	Habicher (2009):
Foraging	Forage, Drink
Cooperative	Vigilant, Social Dig
Inactive	Stationary, Huddle, Sunbathe
Active	Travel, Playfight, Groom, Allogroom
Below	(any behaviour where the location is recorded as inside the shelter, if one is present)
Out of sight	Out of sight
	Other: Keeper Interaction, Object Interaction, Inter-specific Interaction

The significance of the differences in behavioural time budgets between groups was assessed using chi-squared tests as recommended for analysis of activity budgets by Marples et al. (in Plowman, 2006). Chi-squared allows a matrix of "observed" frequencies, for example how often each behaviour occurs in each zoo, to be compared to another "expected" matrix in which the only difference between groups (in the example, the different zoos) is a result of the different number of observations made, and to quantify the probability of the observed differences being a result of random chance rather than a significant trend. The differences between zoo groups, between wild groups, and between the overall measurements for zoo and wild groups were tested. This test assumes independence of samples, which is not the case when the same individuals are being observed multiple times, and/or multiple animals are included in each scan sample, influencing each others' behaviours. I therefore also performed the chi-squared calculations making more conservative assumptions, using an average number of occurrences of each behaviour over each observation session, which consisted of scan samples every two minutes for 20 minutes in the zoo, and scan samples every minute for an hour in the wild, and assumed that each separate session represented an independent sample. This resulted in a smaller sample size, and in some cases expected values lower than five, which is discouraged when using chi-squared; however, the assumptions of

independence were more likely to be correct. To assess how the activity budgets of each group of meerkats differed from the wild, I again performed chi-squared tests using the assumption of independence of observation sessions. To attempt to identify what factors affected how wild-like the behaviour of meerkats in different zoos was, I created a general linear model with the chi-squared value calculated in the previous step as the response variable. I used group size, presence of pups, outdoor enclosure area, indoor enclosure area (see appendix B for data) and the interactions between group size and the other variables as potential explanatory factors, and performed model simplification on this full model. Data for wild groups was kindly provided by A. Habicher, and represents the raw data described in Nienhaus (2009).

To investigate which behaviours differ most significantly between groups, I compared each behaviour separately. For each behaviour a generalised linear model was built with quasibinomial errors, due to overdispersion, with the proportion of scans in which the behaviour was observed for each group as the response variable, and the type of group (wild or captive) as the explanatory variable. To account for multiple comparisons, a Bonferroni adjustment was applied.

3.3.3.3 Effects of group size

A series of generalised linear models were created with group size as the explanatory variable, a quasibinomial family, due to overdispersion, and the mean proportional frequency for meerkats in each social group of each of Vigilance (Vigilant), Grooming (Groom), Social behaviour (Allogroom, Huddle, Interactions, Playfight), Foraging (Forage, Drink), Travelling (Travel), Inactivity (Sit, Sunbathe), inside and out of sight as response variables, with a Bonferroni adjustment for multiple comparisons to reduce the risk of type I errors as as result of performing multiple tests. The mean value for each zoo is used to prevent excessive influence from the larger groups. For inside and out of sight, the mean proportion of all scan samples in which each animal was either known

to be inside or was not visible was used; for the other variables, it was the mean proportion of the time during which each animal was visible outdoors which was used.

3.3.3.4 Sentry behaviour

For each scan sample, all the meerkats were classified as “Raised Guarding” - when they were Vigilant, Sitting or Sunbathing on an elevated position - or not. If only one animal was Raised Guarding, this individual was recorded as the Sentry; if there were no animals or more than one animal in Raised Guard, the scan sample was classified as No Sentry or Multiple Animals Raised Guarding, respectively.

For 33 meerkats (15 females and 18 males) I had data on both their behaviour and their weights. I used the mean proportional difference in captive meerkats' weight from that expected of a wild meerkats of the same age to compare body weight and, firstly, Sentry duty, and secondly, all Raised Guarding (see chapter 5 for more details on weighing methods). Generalised linear models were used to assess the effect of weight on proportion of time spent on Sentry duty and Raised Guarding, with quasibinomial errors and including group size and age as additional explanatory variables.

The effect of social group size on the proportion of time an individual spent on Sentry duty was analysed by building a generalised linear model with quasibinomial error structure, in which the mean proportion of time each animal spent on Sentry duty was related to group size. A similar model was used to analyse the effect of group size on the proportion of scans in which at least one animals was in Raised Guard. The effect of age and sex was analysed with a generalised linear model with quasibinomial errors relating the proportion of each animal's time it spent on Sentry duty and including group size, age, sex and the interaction between age and sex as explanatory factors; the effect of age on each sex was also analysed separately by dividing the dataset by sex

and running the same analysis with age and group size as explanatory factors.

To assess the effect of zoo visitors on meerkats' guarding behaviour, I used a generalised linear mixed model with the proportion of the visible meerkats which were in a Raised Guarding position as the response variable and the number of visitors within two metres of the enclosure as the explanatory variable; social group was included as a random effect and a binomial error structure was used.

3.4 Results

3.4.1 Do captive meerkats behave differently to wild meerkats?

3.4.1.1 Time budgets in captivity

Amongst zoo meerkats, the most common behaviour is Foraging taking up about a quarter of the average captive meerkat's time and a third of its time when outdoors, (see tables 3.1 and 3.2, and figure 3.1). The only two other behaviours which every animal was observed to perform are Stationary (sitting or lying), and Travel (walking or running). There is a high level of variation in the time budgets of different individuals, with the cooperative behaviours Allogrooming, Vigilance and Social Digging being particularly highly variable – the proportion of time spent Vigilant ranged from none to almost half the observations. There was also high variability in the proportion of time during which the animal was inside or not visible, which I hypothesise was mainly due to differences in enclosure design and furniture. This hypothesis is supported by the fact that the proportions of time spent by an individual inside and out of sight are both significantly influenced by the social group they are in, with 96.1% of the variation between individuals in time spent inside and 60.5% of the variation in visibility being explained by their social group (Inside: GLM, quasibinomial family; $F_{9,61}=149.56$, $p<0.001$; Out of sight: GLM, quasibinomial family; $F_{9,61}=10.41$, $p<0.001$). This influence of group on visibility and use of the outdoor

area, most likely as a result of differences in enclosure design and furniture, means that, to make fair comparisons between groups, I will use only the observations in which the animal is visible outside for the rest of the analyses, unless otherwise stated.

Table 3.1: Mean and standard error of proportion of total time spent in each behaviour by seventy individual captive meerkats

Behaviour	Proportion of time spent on each behaviour by individual meerkats			
	Mean	Standard error	Minimum	Maximum
Stationary	11.59%	6.36%	1.45%	32.58%
Travel	11.69%	7.31%	0.94%	43.84%
Forage	25.48%	11.45%	5.45%	46.24%
Drink	0.24%	0.33%	0.00%	1.37%
Groom	2.24%	1.98%	0.00%	9.79%
Allogroom	0.90%	1.33%	0.00%	5.94%
Vigilant	13.12%	11.49%	0.00%	47.95%
Sunbathe	0.27%	0.53%	0.00%	2.96%
Social Dig	0.93%	1.36%	0.00%	7.21%
Huddle	2.22%	1.78%	0.00%	6.58%
Playfight	2.93%	3.12%	0.00%	10.93%
Interactions (Keeper, Object, Inter-specific)	0.40%	0.92%	0.00%	6.06%
Inside	15.06%	19.45%	0.00%	55.27%
Out of Sight	12.95%	9.65%	0.00%	47.49%

Table 3.2: Mean and standard error of proportion of time visible outside spent in each behaviour by seventy individual captive meerkats

Behaviour	Proportion of time spent on each behaviour by individual meerkats			
	Mean	Standard error	Minimum	Maximum
Stationary	16.20%	7.80%	3.60%	38.91%
Travel	17.26%	10.21%	1.33%	47.52%
Forage	34.81%	11.65%	13.51%	57.02%
Drink	0.29%	0.41%	0.00%	1.78%
Groom	2.84%	2.21%	0.00%	9.86%
Allogroom	1.23%	1.65%	0.00%	7.60%
Vigilant	17.62%	12.96%	0.00%	51.99%
Sunbathe	0.34%	0.64%	0.00%	3.46%
Social Dig	1.22%	1.74%	0.00%	9.35%
Huddle	3.64%	3.42%	0.00%	14.41%
Playfight	4.05%	3.85%	0.00%	13.75%
Interactions (Keeper, Object, Inter-specific)	0.49%	1.12%	0.00%	7.24%

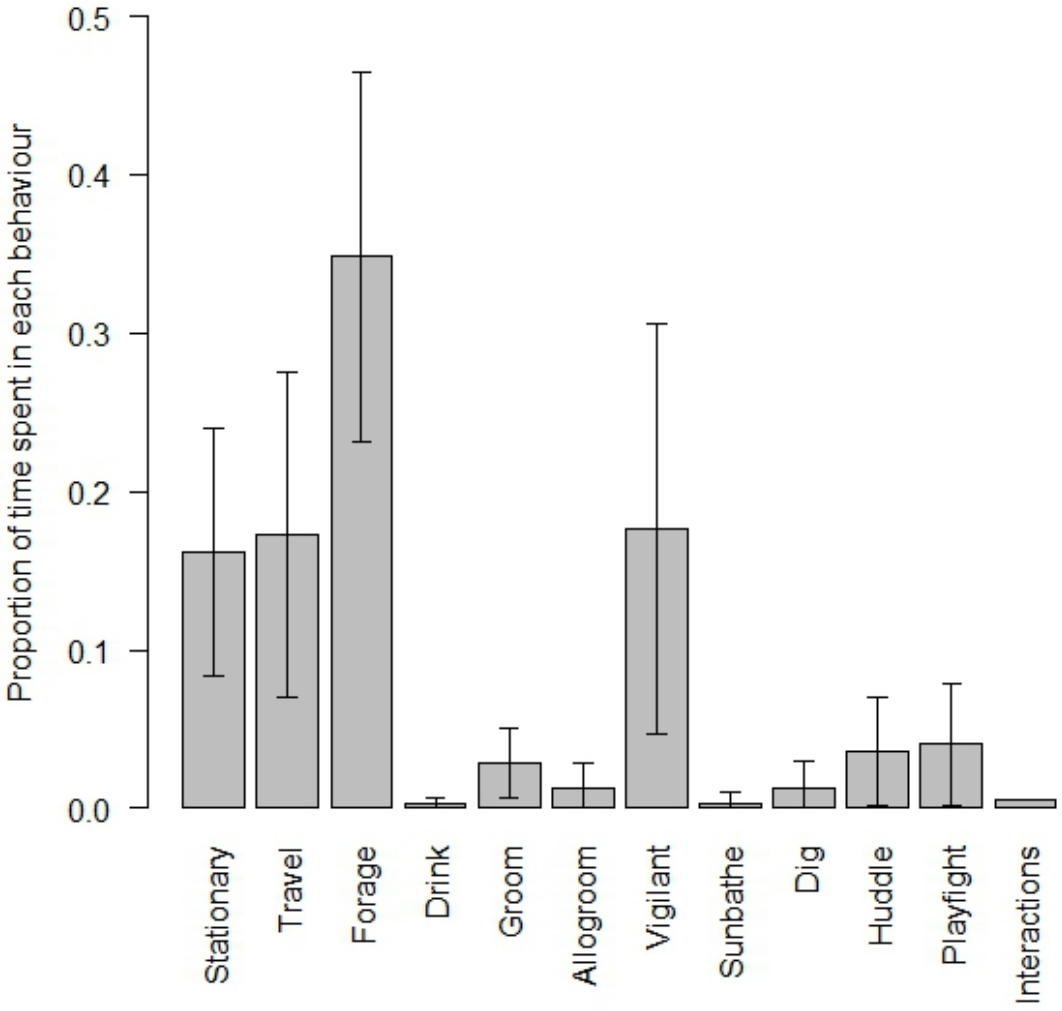

Figure 3.1: The mean proportion of visible outdoor time captive meerkats spend on each behaviour category, with standard deviation between individuals.

3.4.1.2 Comparison to wild time budgets

Assuming independence of samples, when the behaviour of the three wild meerkat groups was compared, the activity budgets were found to be significantly different (χ^2 test, χ^2_{10}=1521, p<0.001, see figure 4 in Nienhaus, 2009). The activity budgets of the ten captive groups were also significantly different to one another (χ^2 test, χ^2_{45}=8961, p<0.001). When the zoo groups are collated and compared to the overall total for the wild groups, the time budgets

were also found to be significantly different (χ^2 test, χ^2_5=68.2, p<0.001, see figure 3.6).

Using the more conservative estimate, with each observation session representing an independent data point, the result were different. The activity budgets of the three wild groups were not significantly different to one another (χ^2 test, χ^2_{10}=3.16, p=0.977), however the differences in behaviour between the ten zoo groups were still highly significant (χ^2 test, χ^2_{45}=113.2, p<0.001). Visual inspection showed that almost half of this difference was a result of the unexpectedly high proportion of time that meerkats at Bristol Zoo spent in their house, which is much larger than that in all but one of the other zoos and includes a visitor viewing area. However, if Bristol Zoo was excluded the differences between activity budgets were still significant (χ^2 test, χ^2_{40}=59.7, p=0.023). The time budgets of the zoo groups were also significantly different to those of the wild meerkats (χ^2 test, χ^2_5=51.4, p<0.001). Here again the largest difference was in the time the animals spent in their house or den, with wild meerkats spending more time underground than their captive counterparts did inside their house, burrow or den; it also appeared that zoo meerkats spent much more time Active than those in the wild, but slightly less time Foraging.

When comparing each zoo individually to the wild activity budget, again using the more conservative assumptions of independence of sessions, a wide range of levels of difference was found (see table 3.3). For five of the ten groups, the difference between their activity budget and that of the wild meerkats was not significant using the Bonferroni correction (α=0.005), while the behavioural budgets of the other five were significantly different to the wild. In four of the five zoos where behaviour was significantly different to the wild, most of this difference was a result of zoo meerkats spending more time Active (a category which includes Travelling, Playfighting, Grooming and Allogrooming) than their wild counterparts. In the fifth, Paignton (pair), Active behaviour was also much higher than expected, but so was Cooperative behaviour (Vigilance and Social Digging).

*Table 3.3: The significance of differences between the activity budget of meerkats in each zoo group and in the wild, assuming independence of sessions; * indicates significance without Bonferroni correction (α=0.05), ** indicates significance with Bonferroni correction (α=0.005)*

	χ^2	degrees of freedom	p-value
Blackpool	9.919	5	0.0776
Bristol	11.26	5	0.0464 *
Cotswold (family)	23.76	5	0.0002 **
Cotswold (bachelor)	14.13	5	0.0148 *
Dartmoor	17.75	5	0.0033 **
Longleat	20.09	5	0.0012 **
Newquay	15.08	5	0.0100 *
Paignton (family)	35.90	5	<0.0001 **
Paignton (pair)	39.09	5	<0.0001 **
Shaldon	3.284	5	0.656

In an attempt to identify causes of this variation in similarity to wild behaviour across different zoos, I used a general linear model with group size, presence of pups, outdoor enclosure area, indoor enclosure area and the interactions between group size and the other variables as potential explanatory factors. None of the variables or interactions were found to have significant predictive power (General Linear Model, group size: $F_{8,1}$=0.772, p=0.405; pups: $F_{8,1}$=0.694, p=0.429; outdoor area: $F_{8,1}$=0.264, p=0.622; indoor area: $F_{8,1}$=1.47, p=0.260; interaction between group size and pups: $F_{6,1}$=0.947, p=0.368; interaction between group size and outdoor area: $F_{6,1}$=1.81, p=0.227; interaction between group size and outdoor area: $F_{6,1}$=0.339, p=0.582).

Considering individual behaviours, groups of meerkats in zoos spent

significantly more time Active than those in the wild, as was suggested by the chi-squared results (generalised linear model with quasibinomial errors; $F_{11,1}$=33.8, p<0.001, see figure 3.6). After a Bonferroni adjustment (α=0.0083), there was no significant difference in the proportion of time spent on any of the other behaviours between zoo and wild meerkat groups, although the difference in levels of Foraging approached significance (Foraging: $F_{11,1}$=7.69, p=0.018; Cooperative behaviours: $F_{11,1}$=1.40, p=0.261; Inactive: $F_{11,1}$=0.317, p=0.585; in house: $F_{11,1}$=2.25, p=0.162; out of sight: $F_{11,1}$=2.93, p=0.115).

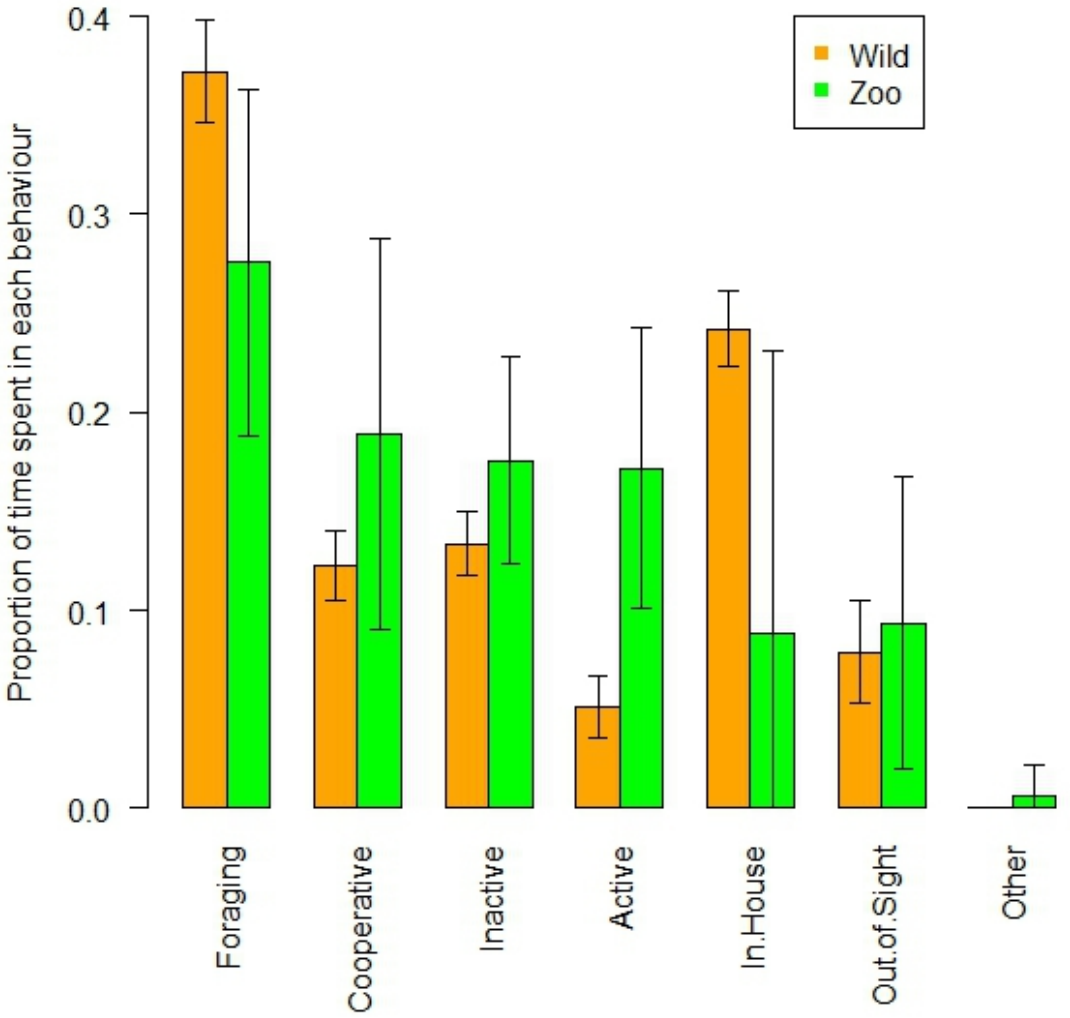

Figure 3.2: Mean proportion of time spent on each group of behaviours by meerkats in the wild (orange) and in zoos (green), with standard deviation between social groups indicated by error bars.

3.4.2 What affects captive meerkats' behaviour?

3.4.2.1 Effects of group size

The proportion of time each individual spent Vigilant decreased as group size increased (GLM, quasibinomial family; $F_{8,1}$=14.3, p=0.005, R^2=0.637, see figure 3.3). The proportion of time spent on Grooming also decreased as groups

became larger, although with the Bonferroni adjustment (α=0.0083) this trend was not significant ($F_{8,1}$=7.19, p=0.028, R^2=0.482, see figure 3.4). Frequency of Social behaviour, Foraging, Travel and Stationary were not influenced by group size (Social: $F_{8,1}$=2.45, p=0.156; Foraging: $F_{8,1}$=0.884, p=0.375; Travelling: $F_{8,1}$=3.33, p=0.106; Inactive: $F_{8,1}$=0.009, p=0.927). Neither time spent indoors nor out of sight changed significantly with group size (inside: $F_{8,1}$=5.04, p=0.055; out of sight: $F_{8,1}$=1.89, p=0.207). These results may be confounded as all behaviours must always add up to one, but since only one activity was found to be significant it is unlikely that any interactions between behaviours are qualitatively altering the results reported here.

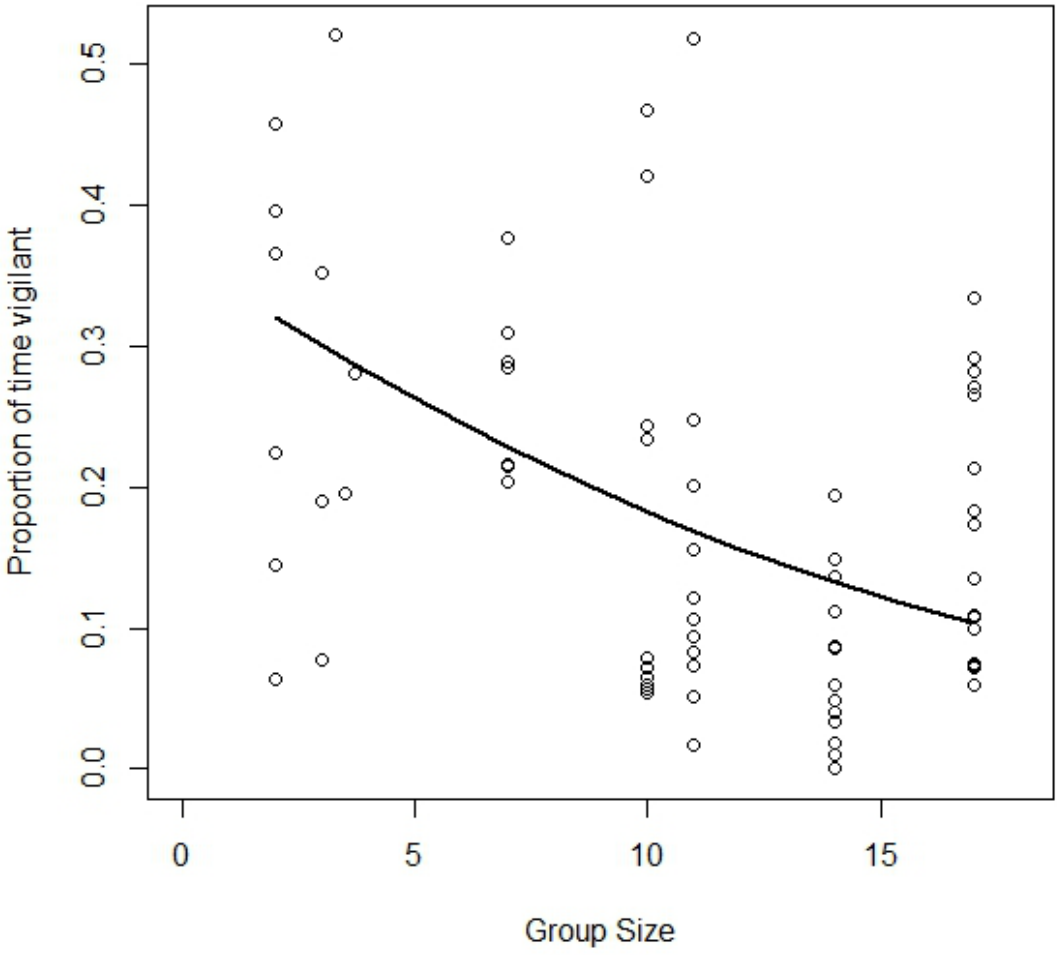

Figure 3.3: Effect of group size on proportion of time each meerkat spends Vigilant

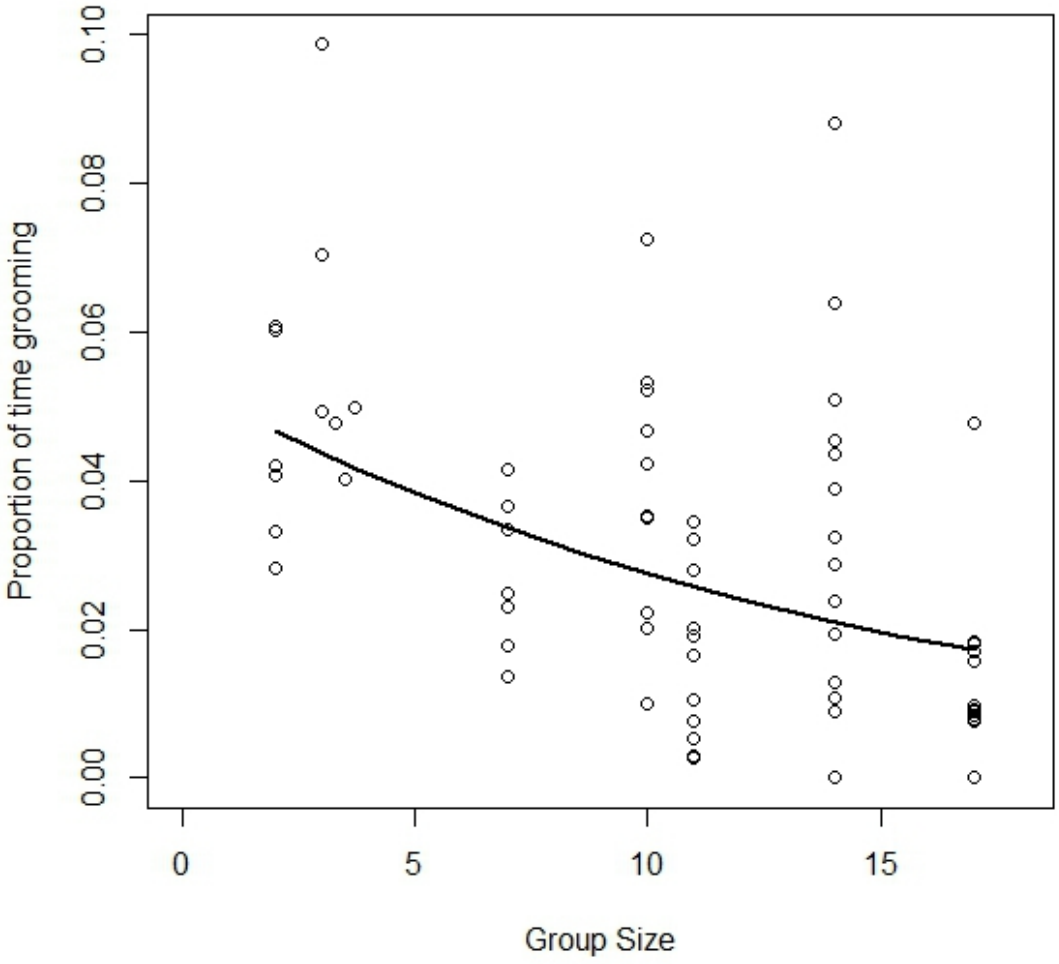

Figure 3.4: Effect of group size on proportion of time each meerkat spends Grooming

3.4.2.2 Sentry behaviour

In the ten zoo groups that were studied, there was no Sentry present for 54.4% of the time (range between groups: 14.6% to 86.8%); one Sentry was present 34.9% of the time (range: 12.2% to 65.0%) and more than one animal was Raised Guarding for the remaining 10.7% of the time (range: 0.0% to 31.6%; n=3575 scan samples, in ten groups). This data can be compared to wild meerkats in an area of high predation risk, which had a Sentinel 55.6% of time,

and those in an adjacent area of low predation risk, which had one 12.0% of the time (Clutton-Brock, O'Riain et al., 1999).

In zoos, the probability that an animal was the sole Sentry was not related to its mean difference from the expected weight, in either sex (GLM with binomial errors; all animals: $F_{28,1}$=1.93, p=0.175; females only: $F_{11,1}$=1.89, p=0.196; males only: $F_{14,1}$=0.488, p=0.496). Nor was the probability of an animal being on Raised Guard at all, solo or not, related to its weight (GLM with binomial errors; all animals: $F_{28,1}$=0.149, p=0.702; females only: $F_{11,1}$=0.673, p=0.429; males only: $F_{14,1}$=0.074, p=0.790).

It was already found in section 3.4.2.1 above that time spent on Vigilance is linked to group size, but this analysis showed that the time an individual spent on Sentry behaviour also decreased significantly as group size increased (GLM with quasibinomial errors: $F_{8,1}$=16.7, p=0.003, see figure 3.5), although the total proportion of time in which at least one animal is in Raised Guard is not significantly affected by group size (GLM with quasibinomial errors: $F_{8,1}$=1.64, p=0.236). The proportion of time spent on Sentry duty was related to the age of the animal, but that relationship differed between males and females (GLM with quasibinomial errors: interaction between Age and Sex: $F_{57,1}$=5.80, p=0.019). Amongst males the amount of Sentry duty did not change with age, but in females the older individuals spent more time on Sentry duty than younger ones (Age (females only): $F_{24,1}$=9.49, p=0.005; Age (males only): $F_{32,1}$=0.025, p=0.875, see figure 3.1). This analysis is confounded by dominance, as there is little overlap in age between dominants and subordinates in these populations.

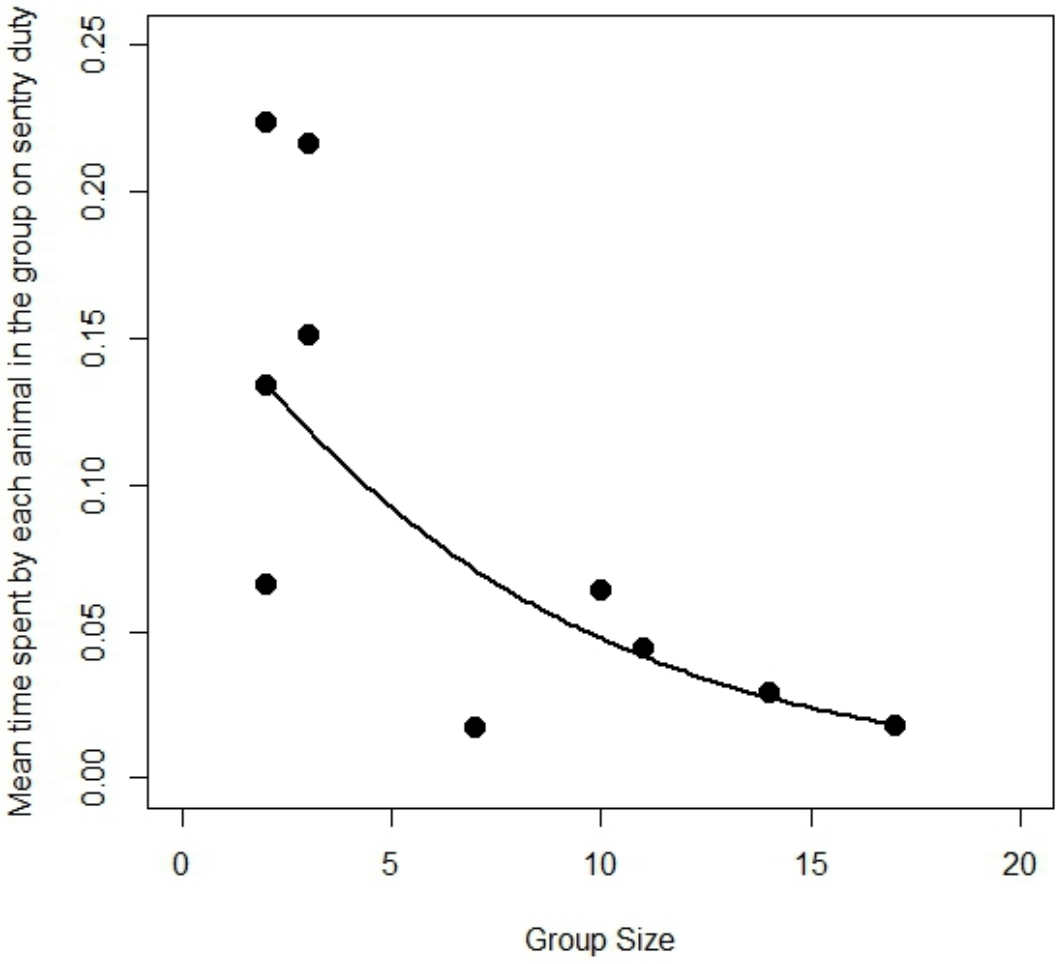

Figure 3.5: Relationship between group size and time spent on Sentry duty by each meerkat.

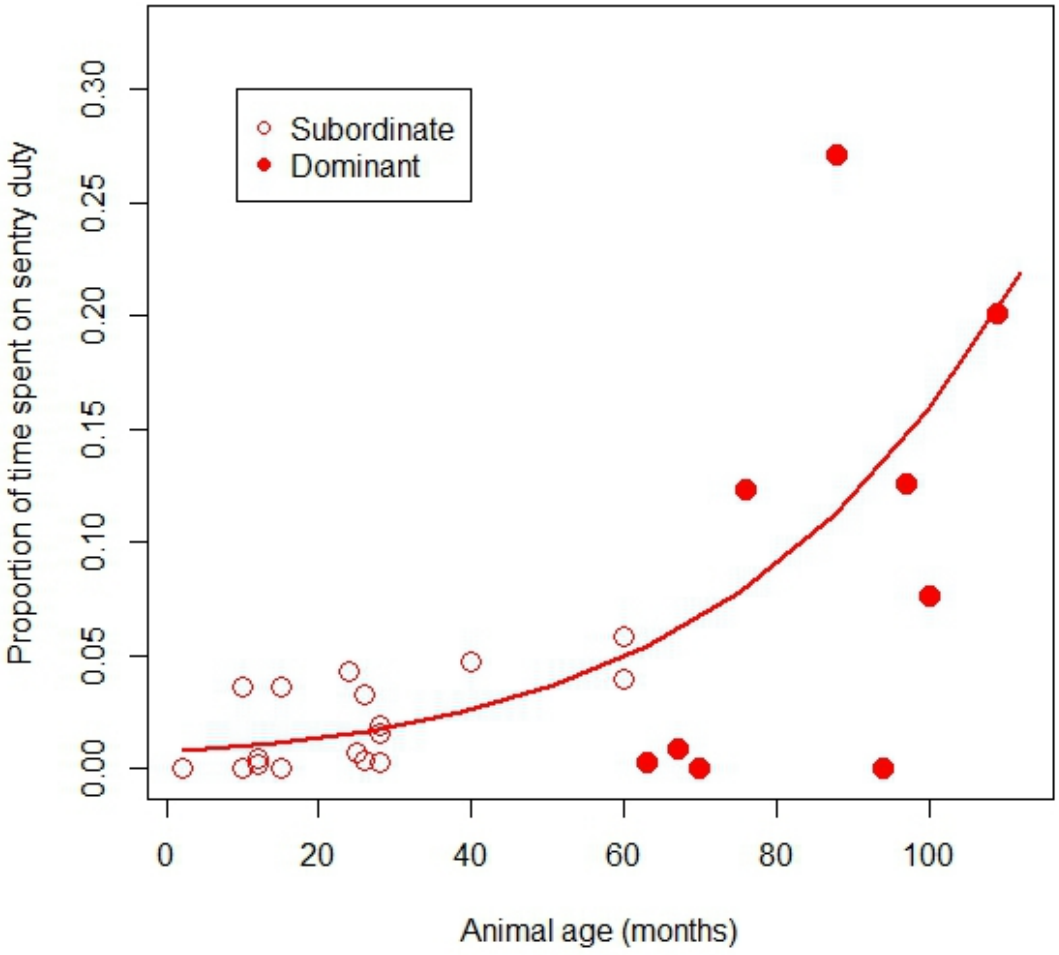

Figure 3.6: Relationship for female meerkats between age in months and proportion of time spent on Sentry duty. Closed circles indicate dominant animals, while open circles indicate subordinates.

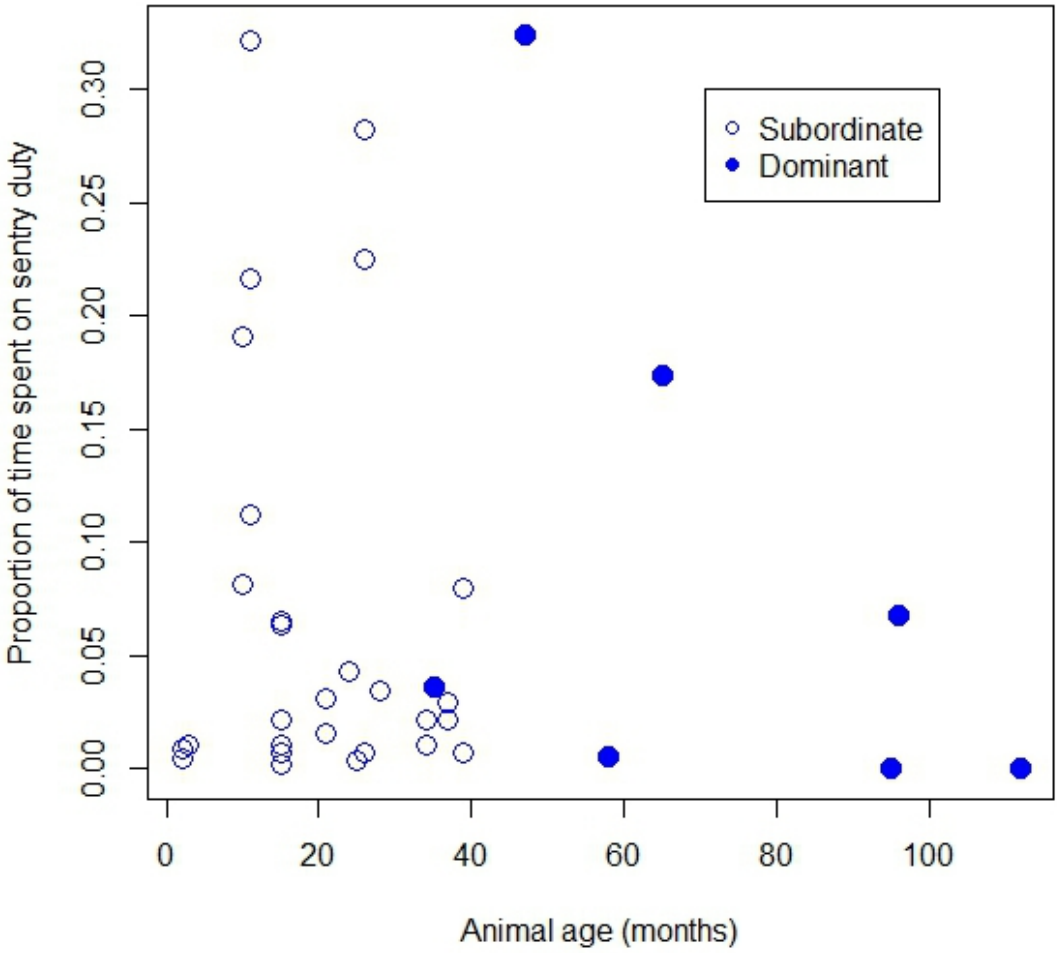

Figure 3.7: Relationship for male meerkats between age in months and proportion of time spent on Sentry duty. Closed circles indicate dominant animals, while open circles indicate subordinates.

When the effect of visitors on Vigilance behaviour was analysed, it was found that fewer animals were in the Raised Guard posture as the number of visitors increases (GzLM with binomial errors and Zoo as random effect; χ^2_1=22.95, p<0.001, see figure 3.8).

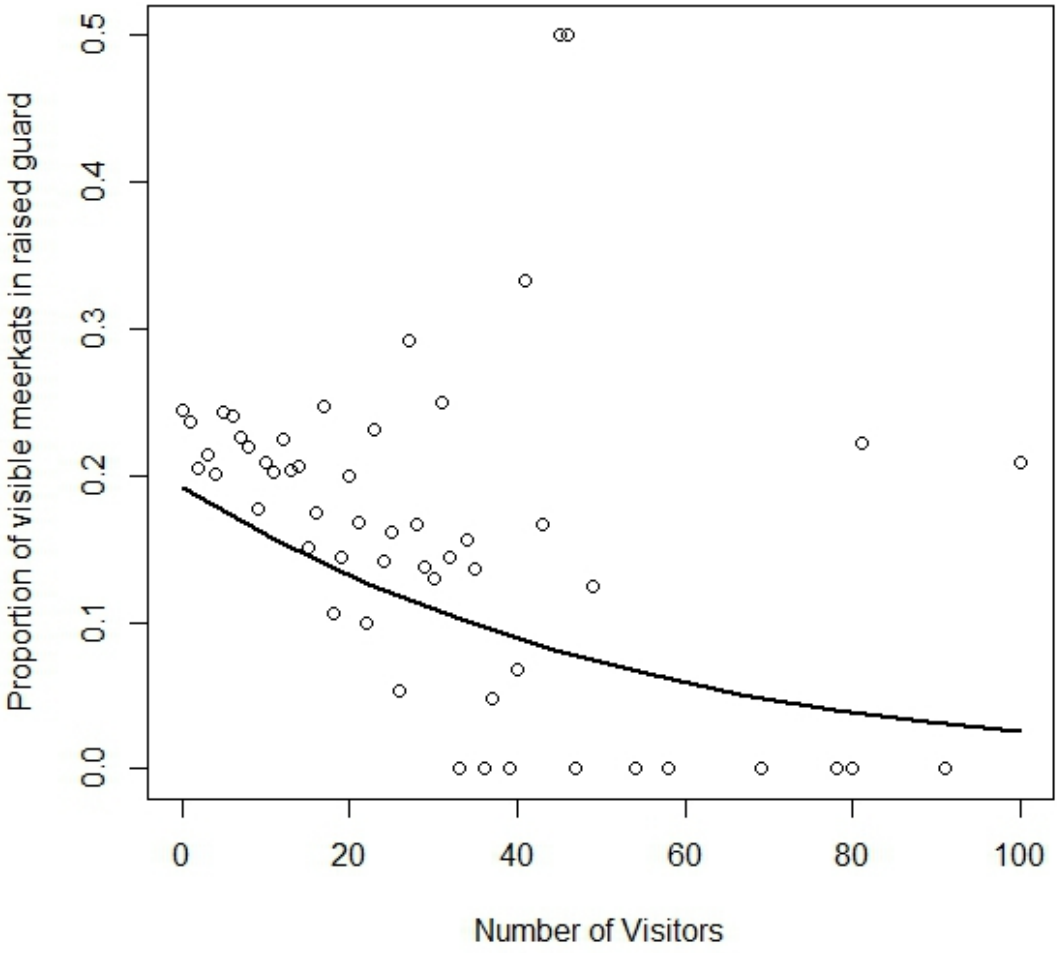

Figure 3.8: Mean proportion of animals in Raised Guard for a given number of visitors within 2m of the enclosure.

3.5 Discussion

3.5.1 Do captive meerkats behave differently to wild meerkats?

The two different groups of chi-squared tests, assuming, first, independence of samples and, second, independence only of observation sessions, gave two different sets of results. In the first case, there was found to be very significant

differences between the time budgets of the wild groups, between the zoo groups, and between the wild and zoo meerkats. In the second case, the wild groups were not found to be significantly different to one another, but there was still significant difference between the zoo groups, and between the zoo and the wild. This highlights the difficulties of using a chi-squared test or similar methods which assume independence of samples in analysis of activity budgets, which are typically measured in ways which cause non-independence. This method is never-the-less commonly used in assessing time-budgets for zoo animals (Plowman, 2006); these results emphasise that such results should be treated with caution. Using the more conservative assumption of independence of observation session should have reduced the potential error, but my calculations of serial correlation (section 3.3.2) shows that, for rare, long-duration behaviours such as Huddling, a twenty minute break between sessions may still not be enough to result in independence of behaviours.

Of the ten captive groups studied, five were found to have activity budgets significantly different to their wild counterparts, but the reason some zoo meerkats were more wild-like in their behaviour than others was not clear. The size of the group, its breeding success, and the size of its enclosure did not seem to be predictive of similarity to wild time budget. The comparisons between zoo and wild activity budgets suggested that the differences were mostly in the proportion of time spent Active, with zoo meerkats spending more time on Travel, Playfighting, Grooming and Allogrooming than wild ones. There is also an almost-significant difference in time spent inside, with zoo meerkats spending less time indoors then their wild counterparts. This is surprising, particularly considering the influences of weather and climate on captive meerkat behaviour, which are discusses in more detail in chapter 4. To summarise, in the captive groups I studied rainfall is a major influence on the amount of time spent inside, and since rainfall is much lower in the Kalahari than in Europe it might be expected that Kalahari meerkats would spend less time inside than those in European zoos. However, wild meerkats may spend more time inside (in their case, underground) than their captive conspecifics because they face a much higher predation threat, so their tunnels are used as

a refuge from predators (Manser and Bell, 2004). In addition, the data of Nienhaus (2009) on wild meerkats was collected between 6am and 8pm, while access to zoo groups is typically only possible between 9am and 6pm; it may be that meerkats spend more time inside in the early mornings and late evenings, accounting for at least some of the variations reported here.

The activity budgets of the ten different zoo groups were significantly different, but much of this difference was the result of one group at Bristol Zoo which used its indoor area far more than would be expected. This was a large, open indoor space with a public viewing area and a large window onto the exterior, and so bore little resemblance to the dens of wild meerkats; tunnels and small “nest boxes” were also provided inside fake termite mounds within the house, and the use of these is likely to more closely resemble the use of dens and bolt holes by meerkats in the Kalahari. When Bristol Zoo was excluded from the analysis, however, there was still a significant, but smaller, difference between groups, suggesting that there are aspects of the zoo environment which vary between zoos and which alter the animals' behavioural time budgets.

Examination of the time budgets of captive meerkats showed that, as is seen in wild meerkats, their most common behaviour when above ground was Foraging, despite the fact that, for the most part, they were fed only two or three times a day. At these feeding times food was suddenly abundant, and so a few concentrated bursts would be expected to provide them with sufficient energy for the day. In fact, the data on weights (see chapter 5) suggests that their energy intake more than meets their expenditure, and so this large proportion of time spent on Foraging must be a result of behavioural "habit" rather than energetic necessity.

3.5.2 What affects captive meerkats' behaviour?

When investigating the causes of behavioural variation between captive meerkats, I concentrated on two areas which captivity might be expected to

alter: the effect of group size, and the occurrence of Vigilance behaviour.

For zoo meerkats, unlike their wild counterparts, the size of the social group is imposed. Group size has been found to influence wild meerkats' behaviour, growth and mortality (Clutton-Brock et al., 2008; Russell et al., 2002; Stephens et al., 2005), and so I was interested to investigate its effects on zoo animals. Although activity budgets were found to vary between social groups of meerkats in captivity (see section 3.4.1.2), the size of the meerkat's group was found not to influence the frequencies of most behaviours; the exception was the time spent on Vigilance behaviour, which is discussed below. The relationship seen between Grooming and group size, which approached significance, is difficult to account for, particularly as Grooming occurred less often as group size increased: a positive relationship might indicate increased levels of parasites in larger groups, but the opposite direction of relationship is observed. In some social species, particularly primates, Grooming is associated with a stress response and displacement activity (Daniel et al., 2008; Troisi, 2002). In studying hormonal stress in captive meerkats, I found that animals in smaller groups had significantly higher levels of glucocorticoids, suggesting higher stress in these meerkats (see chapter 6); this would support the hypothesis that the observed relationship between levels of Grooming and group size is a stress response; investigating this link in more detail would be an interesting direction for future research.

The primary purpose of Sentry behaviour in wild meerkats is to reduce the threat of predation to the sentry and the other members of its group (Clutton-Brock, O'Riain et al., 1999; Tatalovic, 2008). In captivity, the risk of predation is almost non-existent, and yet Vigilance behaviour is perpetuated, including the same alarm calls as are used in the wild (Hollén and Manser, 2007). In the captive groups studied here, a high variation in individual contributions to Vigilance, as well as other Social behaviours, was observed. In all of the ten groups of meerkats observed, a Sentry was posted more often than was observed in a low predation area in the wild (Clutton-Brock, O'Riain et al., 1999). This difference between wild and captive meerkats is likely to be

because nutritional constraints are relaxed in all captive meerkats, as enough food is provided for all of them, and so the different in energy levels available to heavy and light individuals is much less than in the wild. The high level of Raised Guarding in captivity supports Clutton-Brock et al. (2002)'s suggestion that contribution to Cooperative behaviours is governed by energetic state. However, I found no effect of weight, relative to age, as a predictor of the identity of sentries. A likely reason for this is that absolute weight is not a sufficient proxy for energetic state: change in weight over the day would have been a more useful measure of energy balance. Clutton-Brock et al. (2002, 2003) found that it was only during the first year of life that absolute weight acted as a predictor for Cooperative behaviours, and after this point it was daily weight gain which was most closely associated with cooperation. As captive meerkats were not weighed daily, it was not possible to compare this measure directly. It may also be that the feeding regime in the zoos was sufficient that the strict energy constraints experienced by wild meerkats did not apply to captive ones, and so energetic condition was no longer the major predictor of Sentry behaviour (see chapter 5 for more on the growth and weight of meerkats in captivity).

The major influences on Sentry behaviour in captive meerkats were the size of the social group, the animal's sex and age, and the number of zoo visitors present. As is observed in wild meerkats (Clutton-Brock, O'Riain et al., 1999), individuals in smaller groups were seen to spend more time on guard than those in larger groups. The total proportion of time during which at least one Sentry was on guard was not related to group size, so animals in smaller groups were doing a larger proportion of the same amount of work. In the wild, dominant females contribute the least to Sentry duty (Clutton-Brock, O'Riain et al., 1999), but in these captive groups a different trend was observed, with older, dominant females performing much more of the Sentry duty than younger females, while in males age did not affect Sentry behaviour.

The number of visitors present also had an effect on captive meerkats' Sentry behaviour, with more animals being on Raised Guard when there were fewer

visitors present, indicating a distinct visitor effect on the behaviour of captive meerkats which inevitably causes it to differ from the wild (Hosey, 2000). This may have been partly influenced by the fact that the highest number of visitors often occurs around feeding time, when fewer meerkats are likely to be on Raised Guard as they are competing with their neighbours for food. However, in the wild meerkats are known to use heterospecific alarm calls by other animals in the vicinity to alert them of potential predatory threats (Flower, 2011), so perhaps the presence of more humans could be perceived as either lessening the threat of predation or increasing the probability of detecting a predator, and thus reducing the need for Vigilance by the meerkats.

3.5.3 Conclusions

For captive as well as wild meerkats, Foraging is the most time-consuming behaviour despite the provision of food at particular times during the day. Meerkats in zoos, however, spend less time inside or underground and more time on Active behaviours than their wild counterparts. Activity budgets, and the similarity of these to those of wild meerkats, varied markedly between zoos, but the group size, breeding success and enclosure size were not found to be predictive of behavioural patterns. The size of the social group does influence Vigilance behaviour, though, with animals in smaller groups each taking a larger share of the Sentry duty. This suggests that there are behavioural costs of living in a small group, as these animals dedicate more time to Vigilance and therefore have less time for Foraging and Social behaviours. Animals in small groups also spend more time Grooming than those in larger groups, which possibly ties in with the link between group size and stress hormone level which is discussed in chapter 6. The relationship between age, sex and Sentinel behaviour is completely different to that seen in the wild (Clutton-Brock, O'Riain et al., 1999), and the weight of the animal was not found to be predictive of Sentry contribution. The number of zoo visitors, however, did have an effect on Raised Guarding, with fewer animals on Raised Guard when there were more visitors present. The zoo environment, therefore, is having an effect on the behaviour of captive meerkats, and the variation between zoos is significant.

From the data presented here, it need not necessarily be considered a priority to aim to make zoo meerkats' activity budgets more similar to those of wild meerkats. Many behaviours are triggered by external cues, which may not be present in the captive environment. Meerkats are not involved in captive breeding or reintroduction programmes, and breed regularly and successfully in zoos; these are two of the five reasons for promoting wild-like behaviour outlined in section 1.3, and they can therefore be discounted in the case of meerkats. The welfare of captive meerkats is discussed in more detail in Chapter 6, and so I will not go into detail here. The two other reasons for promoting wild-type behaviour are to educate visitors, and to allow valid research to be carried out. The results presented here suggest that, while in some zoos the meerkats' behavioural patterns resemble those of their wild counterparts, in others the observed time budgets are significantly different. For both visitor education and validity of research, it would be preferable for zoo meerkats' behaviour to be as wild-like as possible; therefore the environment of the specific zoo group must be considered when judging the wider relevance of experimental observations performed on zoo meerkats, and their application to meerkat behaviour more generally.

4 Seasonal Differences in the Behaviour of Meerkats in Zoos

4.1 Abstract

The effect of temperate climates on the behaviour of desert animals in zoos has been studied remarkably little. Meerkats are a desert species which are commonly kept in outdoor enclosures in northern Europe, where the colder and wetter climate requires different thermoregulatory behavioural responses. I collected behavioural data on meerkats in three zoos in south-west England during both the summer and winter and compared them to published data on meerkats' behaviour in the wild. In the winter, the zoo meerkats spent much more time inside or out of sight than occurs in the wild, and less time foraging. Zoo meerkats seemed to use the 'vigilance' posture, with their undersides exposed to the sun, for thermoregulation, particularly on cold but sunny days. Social interactive behaviours occurred more often outside during the summer than the winter. In one zoo the animal could be seen while inside, and the total time spent on interactive behaviours while inside was higher than when outside both in summer and in winter; this meant that the total amount of time spent interacting was not significantly different between seasons. Rain also had an influence on behaviours, with more time being spent inside or out of sight when it was raining, and less of the time that was spent outside in the rain being used for social interactions. The influence of temperature and rain on the performance of interactive behaviours in a highly social species may have consequences for social structures, but the provision of heated indoor spaces seems to alleviate this without compromising the animals' thermoregulation. In the wild, the effects of seasonal and climatic changes on the behaviour of meerkats are generally linked to the abundance of food; in zoos, this connection is severed but I show here that the season still affects meerkats' behaviour.

4.2 Introduction

Historically, it was thought that tropical animals kept in zoos in Europe and North America required costly heated indoor enclosures which mimicked the temperature and humidity of their native range; however, as long ago as 1902 Carl Hagenbeck, developer and proponent of the “Hagenbeck revolution” in zoo design (see Introduction for more details), while trying to make enclosures resemble more closely their occupants' natural habitat, also advocated the acclimatisation of animals to the weather of their new location (Hediger, 1950, p. 79; Rothfels, 2002, p. 162). This allowed enclosures to be much larger, and also reduced the spread of diseases which incubated in the warm, moist, recirculated air tropical houses of the Victorian era (Exner and Unshelm, 1997; Hosey et al., 2009, pp. 187–190). In modern zoos, it is common for mammals which evolved in tropical or desert regions to live in outdoor enclosures exposed to the climate of their new environment; however, there has been remarkably little research on the effect on zoo animals of living in a climate for which, evolutionarily, they were not adapted (Hosey et al., 2009, p. 529; Melfi, 2009).

Mammals and birds maintain their bodies at a constant temperature, often at a high energetic cost. This thermoregulation is particularly costly when the ambient temperature differs significantly from the animal's thermoneutral zone (Habicher, 2009). Within the thermoneutral zone (TNZ), basal metabolic activity and control of skin blood flow is sufficient to maintain the core body temperature at its proper level; however, once the ambient temperature falls below this level it is necessary to increase metabolic rate, and therefore expend more energy (Habicher, 2009). Species which evolve in climates which are often colder than the lower limit of their TNZ have adaptations to counter this, both morphologically (for example thick fur) and behaviourally (such as hibernation). However, captive animals may not have the appropriate adaptations for the climate they live in: cases of frostbite have been recorded in rhesus macaques kept in captivity, with subordinate animals which cannot access monopolised heat sources as the worst affected (Hutchins, 2006; Morgan and Tromborg,

2007) Many species exhibit stress reactions when faced with extreme temperatures at either end of the scale, while variation even within their comfortable temperature range can alter the behaviour of various species: across a range of species, huddling behaviours are more common at low temperatures while playing and aggression are more common when it is warmer, while behaviours associated with stress such as distress calls and stereotypies also occur in some species when the temperature is outside their preferred range (Morgan and Tromborg, 2007; Rees, 2004). The frequency of olfactory behaviour in female black rhinoceros has also been linked to climate, with rhinoceros in warmer climates performing the behaviour less often (Carlstead, Fraser et al., 1999). Captive Asian elephants, too, exhibit different behaviours depending on the temperature, with stereotypies decreasing and dust-bathing increasing as temperatures rise (Rees, 2002, 2004). Behaviour of zoo animals might likewise be expected to vary in response to rainfall, although this seems to be rarely documented (Melfi, 2009).

In this chapter I investigate the effect of climate on the behaviour of captive meerkats using data on groups in three zoos in the south-west of England in both summer and winter, and comparing the behavioural repertoires of these groups with existing data on behavioural patterns of wild meerkats. Meerkats are a species of social mongooses found in arid regions of southern Africa (Clutton-Brock et al., 2001). Their typical habitat experiences distinct dry and wet seasons each year, with very low humidity in the dry season and high fluctuations between daytime and night-time temperatures throughout the year (Habicher, 2009; Russell et al., 2002) (see figure 4.1). In the Kuruman River Reserve, average annual rainfall is around 250mm per year (http://www.kalahari-meerkats.com/index.php?id=krr). In the wild, temperature and rainfall have been shown to affect breeding success, pup growth and adult meerkat weight (Doolan and Macdonald, 1997; English et al., 2012), which in turn influences the exhibition of social and cooperative behaviours (Clutton-Brock et al., 2000; Russell et al., 2002). Meerkats are physiologically adapted to a desert environment, having a very narrow TNZ of 30°C-33°C and low basal metabolic rate to cope with high temperatures (Habicher, 2009). To reduce the

metabolic cost of coping with low temperatures, they perform a number of behaviours to reduce heat loss: sunbathing, contact lying (to conduct heat to a cooler surface), huddling, piloerection, and sheltering from rain (Habicher, 2009).

Meerkats in captivity can experience a very different climate to that of their wild habitat. All three meerkat groups which I studied were situated in the south-west of England and experienced a similar climate to each other, with temperatures in summer reaching around 22°C, but rarely dropping below freezing in the winter. Rainfall is much higher than in the Kalahari, and occurs all year round (see figure 4.1).

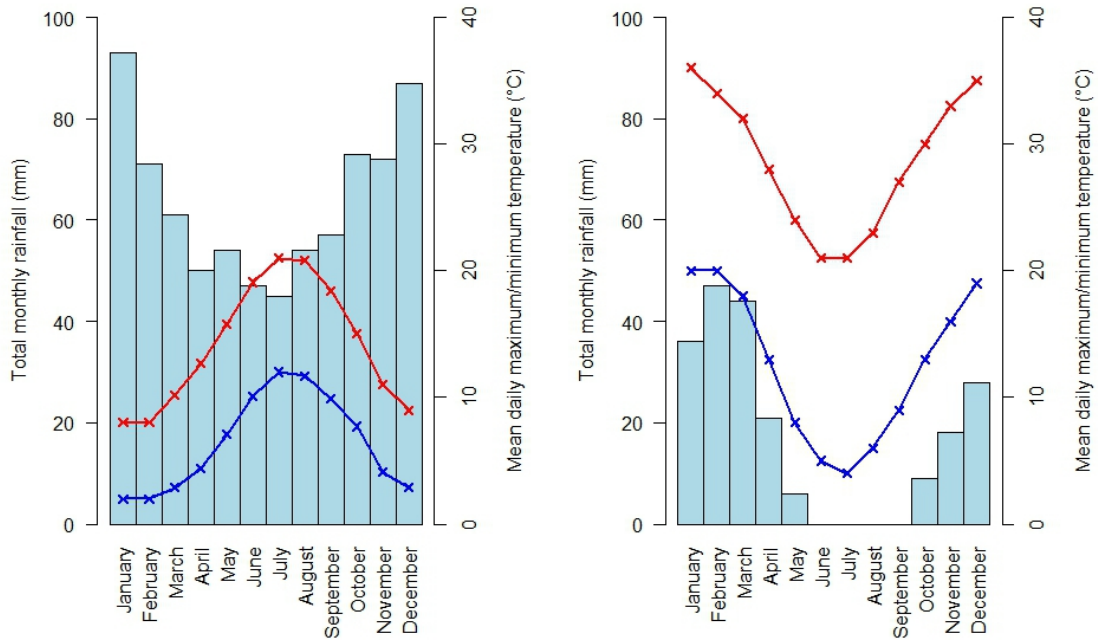

Figure 4.1: Climate in the south west of England (left) and in the Kalahari (right), with rainfall shown in bars (scale on left axis) and mean daily minimum and maximum temperatures shown as points (scale on right axis); scales are identical in the two figures (SA Explorer, n.d.; World Meteorological Organization, n.d.).

The specific objectives of this study were to answer four questions about how the behaviour of meerkats differed between seasons and under different

climatic conditions.

Question 1: Do the time budgets of meerkats in zoos differ significantly from those of wild meerkats? Since captive meerkats are fed by keepers and therefore need to do less work to obtain nutrition, I predict a) that captive meerkats would spend less time foraging than wild ones (although all the zoos for which I have information about feeding regimes do include some live scatterfeeding, so captive meerkats still have to work for their food); b) that the differences in behavioural budgets between wild meerkats and captive conspecifics during winter will be more pronounced than during summer, as British winter weather is more unlike the Kalahari climate than British summer weather; and c) that in winter, more time will be spent inside or underground than in summer or in the wild.

Question 2: Does the "vigilance" posture play a role in thermoregulation? During cold but sunny weather, it is often noticeable that multiple animals stand on their hind feet in the "vigilance" posture, with their underside facing the sun, suggesting this behaviour plays some part in thermoregulation. By comparing the mean proportion of animals in this posture at different temperatures when it is sunny and when it is overcast we can determine how much of this behaviour is thermoregulatory. I hypothesise that the vigilance posture will be performed at a baseline level regardless of temperature, but will occur more frequently in cold temperatures if the weather is sunny than if it is cloudy.

Question 3: Does the occurrence of social behaviours differ between seasons? Specifically, I predict a) that huddling will occur more often in winter, as it appears to have a thermoregulatory role; b) that play-fighting and interacting with keepers and other animals will occur more often in the summer, as they are high-energy activities, and in the winter energy is more highly conserved in order to help regulate body temperature; c) that allogrooming, an affiliative behaviour which is useful in strengthening bonds between individuals (Kutsukake and Clutton-Brock, 2006, 2010) will be observed at similar levels throughout the year.

Question 4: How does rain affect meerkats' behaviour? I predict that zoo meerkats will spend more time underground or inside when it is raining, and the time they do spend outside will be primarily on behaviours which are location-specific, such as foraging, vigilance and digging, rather than those which can be performed undercover, such as grooming, huddling and inactivity.

4.3 Materials and Methods

4.3.1 Study populations

Observations were made of 22 meerkats in three zoos in the south-west of England, first during summer, and then again during the following winter. All animals could be individually recognised by either natural distinctive features or a small hair-dye mark placed on the animals at the beginning of the study, following the methodology used at the Kalahari Meerkat Project (Carlson et al., 2006; S. Hodge, pers. comm.). In each zoo, scan samples of all individuals were performed every two minutes for 20 minutes, recording the location and activity of each animals (for ethogram, see appendix A) and the number of visitors, weather, and presence of predatory birds or aircraft were recorded. This was followed by at least a 15 minute gap before the next data collection session. Temperature data were retrieved from weather stations local to each zoo via the Met Office (www.metoffice.gov.uk). The social structures and data collection periods were as follows: Newquay Zoo's group consisted of a non-breeding group of mother and 10 adult (more than 1 year old) offspring (4 males and 7 females in total), and summer data were collected between 4th and 12th August 2011, when daytime temperatures ranged between 10°C and 20°C. The winter data collection session occurred between 25th January and 3rd February 2012, by which time two of the female offspring had been moved to another zoo (4 males, 5 females); daytime temperatures during this period ranged from 0°C to 10°C. Paignton Zoo's meerkat group consisted of a breeding pair and their two pups (2 males, 1 female, 1 unknown), and summer data were collected between 28th August and 9th September 2011, with daytime temperatures

between 14°C and 20°C; during the study period, one of the pups of unknown sex died and the adult male was temporarily taken into the vet centre before being returned to the group, resulting in varying group sizes through the study. In the winter, the remaining three animals (2 males, 1 female) were observed from 19th to 29th December 2011, when temperatures ranged from 7°C to 13°C. Shaldon Wildlife Trust's group contained a mother and six adult offspring (3 males, 4 females in total), and data were collected between 31st August and 9th September 2011, with daytime temperatures ranging from 15°C to 22°C. The same animals were present in the winter session between 21st and 28th February 2012, when temperatures were between 8°C and 16°C.

4.3.2 Do the time budgets of meerkats in zoos differ significantly from those of wild meerkats?

Wild data on time budgets were taken from Habicher (2009). This wild data is the same data used by Nienhaus (2009) which was quoted in Chapter 3, but is analysed with an emphasis on thermoregulatory behaviours, making it more useful for comparison in this context. This data was collected between December and February, which is the Kalahari summer. To accord with the wild data collected by Alex Habicher and Yvonne Nienhaus (Habicher, 2009), behaviours were recorded using the ethogram included in appendix A, but were then grouped into five categories: Foraging, Cooperative, Thermoregulation, Other and Out of Sight. “Cooperative behaviour” consists of behaviours which benefit the group as a whole: vigilance and social digging. “Thermoregulation” refers to sunbathing and huddling. “Other” includes moving, grooming, not active and play-fighting. In both wild and captive analyses, time out of sight, underground or (for zoo meerkats) in their house was included. Habicher (2009) divided wild animals which were not visible into those that are “Below” (i.e. below ground) and “Out” (i.e. out of sight, possibly but not certainly below ground). I combined these categories for analysis; “Below” accounts for about 80% of the combinded category. To compare proportion of time in a behaviour between wild and captive meerkats, generalised linear mixed models were used

with a binomial error structure to account for the proportional nature of the data and with Zoo as a random effect. A GLMM was run for each behaviour independantly, which increased the risk of false positive results so a Bonferroni correction was applied (α=0.005). For comparisons between summer and winter behaviour in zoos, paired t-tests were used, excluding data from the two meerkats which were only present in summer. There was no need for a mixed model including Zoo as a random factor, since each animal was being compared to itself in the other season, and therefore the effects of zoo in both cases were the same.

4.3.3 Does the "vigilance" posture play a role in thermoregulation?

The proportion of meerkats in the "vigilance" posture in each scan was modelled in a generalised linear mixed model with binomial errors and Zoo included as a random effect, with temperature (rounded to the nearest degree) and weather (sunny or not, determined by whether or not any meerkats not undercover cast a shadow) included as explanatory variables. There were 2833 scan samples available for analysis. The same analysis was repeated for only those scans which occurred when it was sunny (774 scans), and only those when it was overcast (2059 scans), to assess the effect of temperature in each of these conditions.

4.3.4 Does the occurrence of social behaviours differ between seasons?

The proportion of time each animal spent in social interactive behaviours, of the time it was visible above ground and not in its indoor enclosure, was compared across seasons using paired t-tests. Play-fighting, huddling, allogrooming and interacting with keepers or other species in the enclosure (peacocks, seagulls) were classified as social behaviours, because they all required the meerkat to interact with and react to another animal rather than just being driven by its own internal behavioural drives. The two animals for which data was not available in both summer and winter were excluded from the analysis.

In one zoo, Newquay, it was possible to reliably observe the behaviours of meerkats when they were inside their house. This data was used to analyse the differences in levels of social behaviour inside and outside. The effect of season, location (indoors or outdoors) and their interaction on proportion of time each animal spent on all social behaviours were analysed using a generalised linear mixed model, with a binomial distribution and including animal ID as a fixed effect.

4.3.5 How does rain affect meerkats' behaviour?

The proportions of time captive meerkats spent out of sight when it was raining and when it was dry were compared using a two-sample t-test, with the number of animals inside or out of sight when it was raining compared with the number inside or out of sight when it was dry. The time budgets for all meerkats combined during wet and dry weather were compared with a chi squared test, which compared the number of animals observed performing each behaviour when it was raining and when it was dry to the number that would be expected if the weather was not affecting the time budget. The behaviours which were most different between conditions, identified as those with the highest $(O-E)^2/E$ values under both conditions, were compared using two-sample t-tests. This allowed me to focus on the behaviours which seemed to be influencing the difference in time budgets most strongly, while keeping the risk of type I errors as low as possible.

4.3.6 Statistical analyses

Statistical analyses were performed in R 3.0.1 (R Development Core Team 2013) and in excel following standard procedure for performing Student's t-test.

4.4 Results

4.4.1 Do the time budgets of meerkats in zoos differ significantly from those of wild meerkats?

The general pattern of behaviour distribution was similar in wild and zoo meerkats, with the most common activity when they were above ground being foraging. Zoo animals were not found to spend significantly more or less of their time in any of the five behavioural categories in European summer or winter than the wild animals did in the Kalahari summer, once a Bonferroni adjustment had been applied to account for multiple models ($\alpha=0.005$). However, zoo animals did spend significantly less of their outside time in thermoregulation than wild animals, if we use the standard probability level $\alpha=0.05$ (GLMM with binomial errors and Zoo as a random effect: $\chi^2_1=4.02$, $p=0.045$). In the winter, zoo meerkats spent more time out of sight than the same animals did in the summer (paired t-test: $t_{18}=2.19$, $p=0.042$), but once again this difference would not be significant if a Bonferroni adjustment were applied.

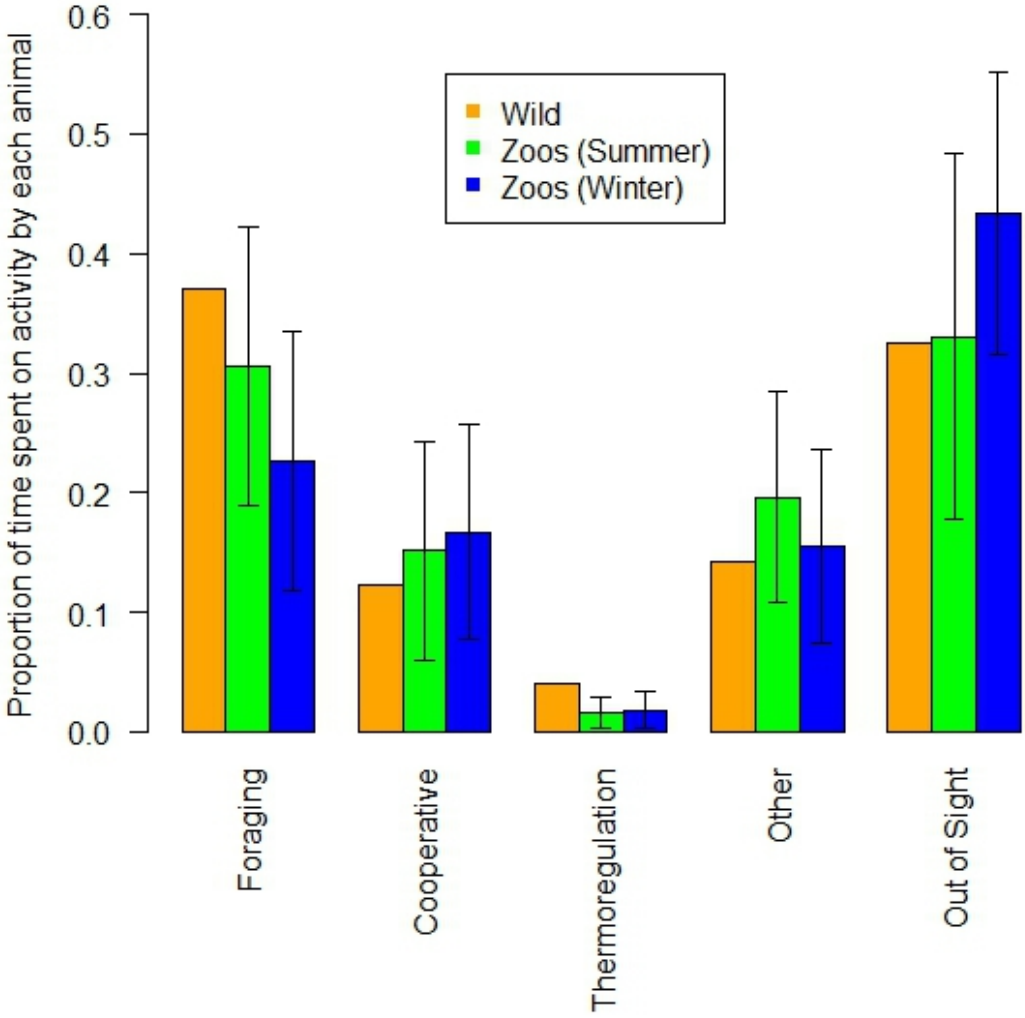

Figure 4.2: Mean (and standard error for captive populations) proportion of time spent by meerkats in the wild and in captivity in summer and winter on different aspects of their behavioural repertoire. The behaviours included in the "Other" category are moving, grooming, not active and play-fighting.

4.4.2 Does the "vigilance" posture play a role in thermoregulation?

The effect of temperature on number of animals standing on hind legs is
2075 significantly different if it is sunny or not (all GLMMs with binomial errors and zoo as a random effect: χ^2_1=299.19, p<0.001). When it is sunny, more animals stand on their hind legs when it is cold (χ^2_1=299.74, p<0.001). When it is not

sunny, fewer animals stand on their hind legs when it is cold (χ^2_1=57.54, p<0.001) (see figure 4.3).

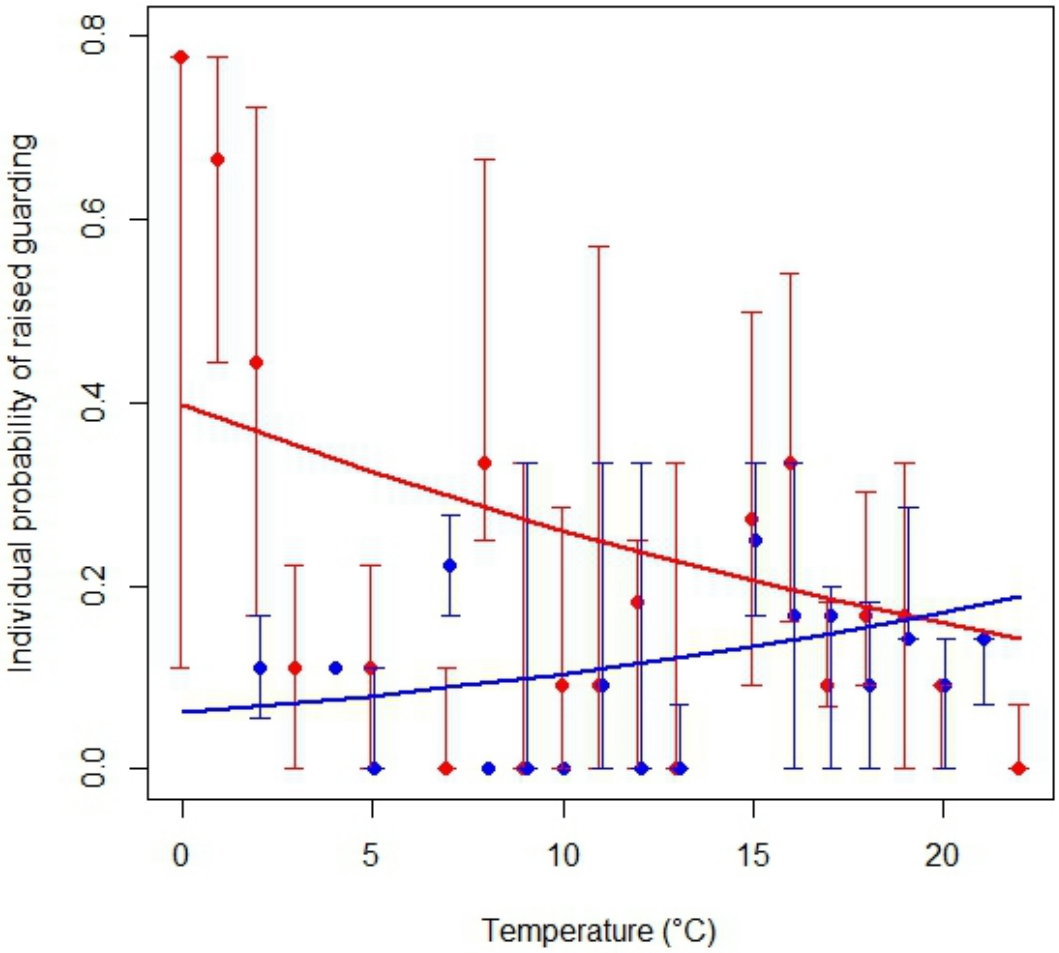

Figure 4.3: Median (and quartiles) proportion of animals standing on their hind legs related to temperature, with data divided between sunny (red) and overcast (blue) weather and lines illustrating the GLM.

4.4.3 Does the occurrence of social behaviours differ between seasons?

Meerkats in captivity spend more of the time they are above ground on all four social or interactive behaviours in summer than in winter (paired t-tests:

allogrooming t_{18}=2.60, p=0.018; huddling t_{18}=3.79, p=0.001; inter-species interactions t_{18}=2.13, p=0.048; playfighting t_{18}=3.40, p=0.003; see figure 4.1).

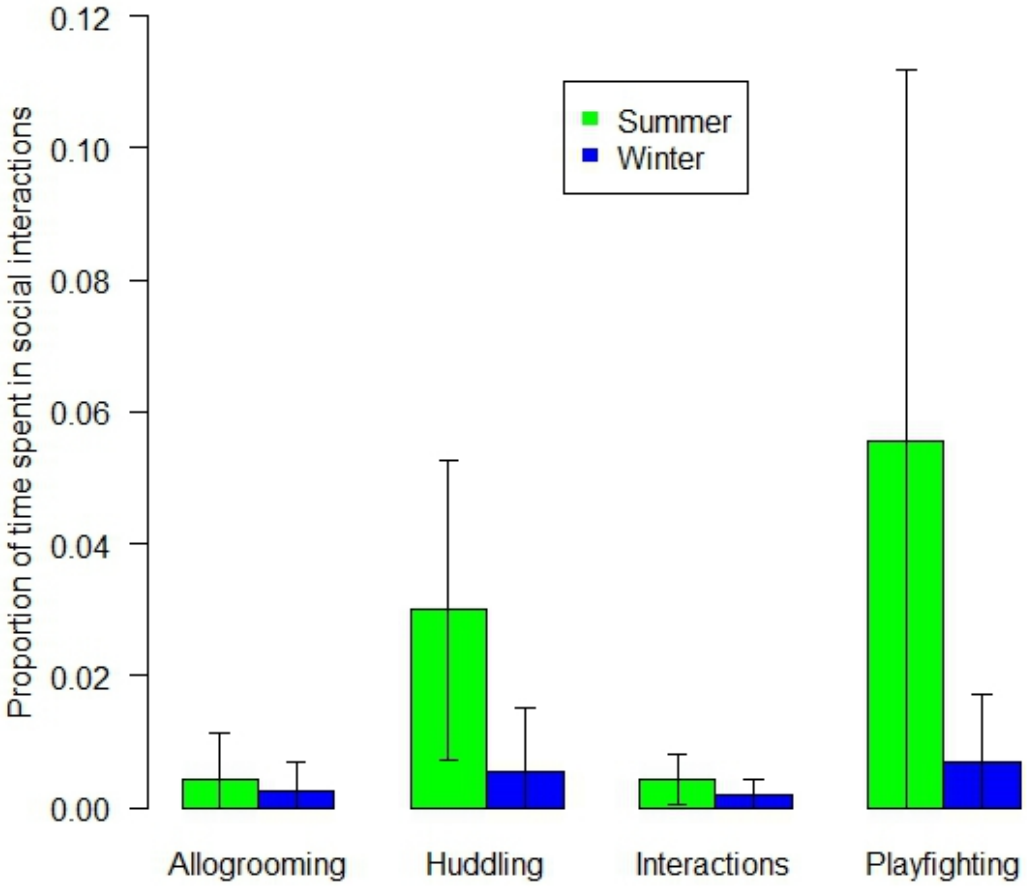

Figure 4.4: Mean (and standard error) proportion of time above ground spent in four key social behaviours by meerkats in zoos in summer and winter. The "Interactions" are with members of other species, such as humans, seagulls and peacocks.

2085 Meerkats in captivity spend more time on social behaviours in the summer than in the winter when they are outside, but they spend more of their time out of sight – much of which time is in their house. At Newquay Zoo, where it was possible to observe the meerkats' behaviour in most of their indoor space, the

proportion of time spent on social behaviours when indoors was significantly higher than that spent on social behaviours outdoors, both in summer and in winter (both GLMs with quasibinomial errors; summer: $F_{1,9}$=127.8, p<0.001; winter: $F_{1,8}$=84.9, p<0.001). The Newquay Zoo meerkats spent significantly more time indoors in winter than in summer (GLM with quasibinomial errors: $F_{1,8}$=424.2, p<0.001). Taking this difference into account, this meant that at Newquay Zoo the total amount of time meerkats spent on social, interactive behaviours was not significantly different between seasons (GLM with quasibinomial errors: $F_{1,8}$=0.617, p=0.455).

4.4.4 How does rain affect meerkats' behaviour?

When it is raining, more time is spent out of sight, under-ground or in the house (when raining (mean ± SE): 55.3%±40.6%; when dry: 31.8%±33.4%; 2-sample t-test: t_{2832}=8.78, p<0.001). When above ground, time budgets are significantly different when raining to when dry (χ^2_6=32.34, p<0.001), with the largest difference being that less time is spent on social behaviours (2-sample t-test: t_{2831}=3.51, p<0.001) (see figure 4.5).

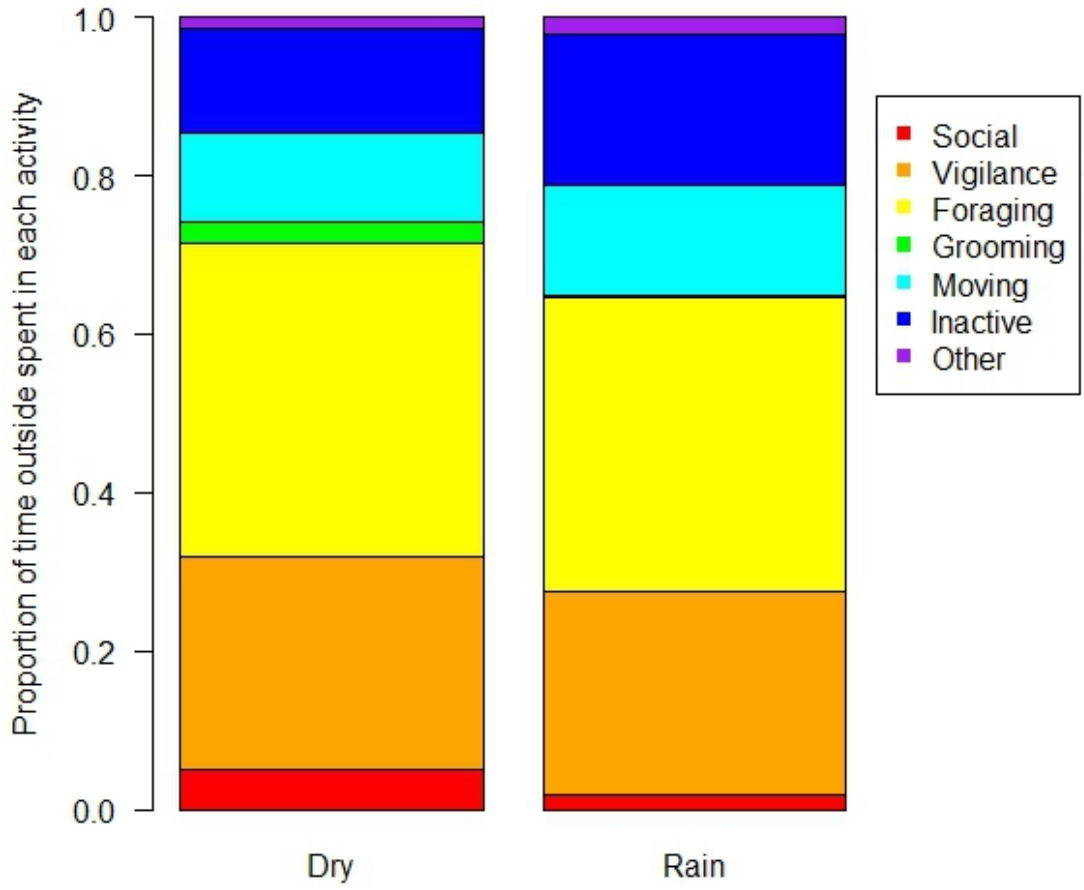

Figure 4.5: Overall time budgets of zoo meerkats when it is raining and dry, excluding time spent out of sight, underground or indoors.

4.5 Discussion

Meerkats in zoos in the United Kingdom generally exhibit a similar time budget to their conspecifics in the wild, although the differences between wild and captive time budgets are greater in winter, when the weather they experience is more unlike that of the Kalahari. The weather in winter in the UK is typically colder and than at any time of year in the Kalahari (see figure 4.1). As might be expected, captive meerkats, which are provided with food, spend less time

foraging than wild ones, although their growth rate and mass tend to be higher than wild conspecifics (see chapter 5), suggesting that either they take in as much or more energy in this shorter time period, or that they do not use up as much energy through the rest of the day, leaving them with a positive energy balance (Doolan and Macdonald, 1996; Scantlebury et al., 2004). Previous research on diurnal mammals in zoos has also found that, along with climatic factors, the regular provision of food plays an important role in determining behavioural patterns (Cooper and Withers, 2004; Hogan et al., 2011). As food supply is related to meerkats' ability to thermoregulate, in the plentiful environment provided in captivity it is likely that the effect of extreme temperatures would be minimised (Doolan and Macdonald, 1996; Müller and Lojewski, 1986).

Thermoregulation has been identified before as a key driver of behaviour in many captive species, including meerkats (Cooper and Withers, 2004; Habicher, 2009; Hogan et al., 2011; Rees, 2004). Captive meerkats exhibit various thermoregulatory behaviours to help them cope with the difference in climate between their ancestral habitat and that which they experience in their current location (Habicher, 2009). While the thermoregulatory behaviours which are observed in the wild, huddling and sunbathing, are seen less often in zoos, when it is sunny meerkats appear to use their vigilance behaviour to maximise their opportunity to absorb heat from the sun. From personal observation, they most often stand with their dark underbellies facing the sun, and it is not unusual to see a whole row of meerkats in the same posture, which would suggest that the primary purpose was not to watch for attack. In addition, when there is no sunlight to warm the animals, they are less likely to assume this posture, suggesting that a "vigilant" animal is losing heat in cold weather.

Meerkats in zoos tend to avoid rain by going underground (or, the equivalent, into their house) when it is falling, as do their wild conspecifics (Habicher, 2009). The time they do spend outside in rain is primarily used for behaviours which are location-specific and cannot be performed inside: foraging and vigilance. In the wild, rainfall strongly correlates with breeding success, but this relationship

is probably due to the increase in food availability which results from a particularly wet rainy season – a correlation which is not applicable to zoo conditions (Doolan and Macdonald, 1996; English et al., 2012). They perform very few social interactive behaviours outside in the rain. These social interactive behaviours are also much rarer in winter than in summer. Even huddling, which, as a thermoregulatory behaviour, might be expected to occur more often during the winter, is seen less in winter than in summer, at least when the animals are outside (Doolan and Macdonald, 1997).

However, from the one zoo for which I have data on their behaviour inside their house as well as outside, the meerkats appear to compensate for their lack of interactive behaviours outside in the winter by performing more of these social behaviours inside. In the wild, too, it is thought that huddling and allogrooming are common behaviours inside the burrow (Doolan and Macdonald, 1997, 1999). The increase in social behaviours when inside during winter suggests that the meerkats are adjusting their behaviour indoors to allow them to perform these social behaviours throughout the year; and also that the provision of indoor space in the zoo allows them to maintain a constant level of interaction through the year, regardless of weather patterns. Since social behaviours, and particularly allogrooming, are known to play a significant social function in maintaining dominance ranks and reducing antagonism, the continuation of these behaviours through the winter may have an important role in maintaining the cohesion of the group (Kutsukake and Clutton-Brock, 2006, 2010; Madden and Clutton-Brock, 2009).

Overall, the results of this study show that meerkats' behaviour is affected by the weather they experience, and this means that captive animals behave in ways which are noticeably different from their wild conspecifics. This difference is exacerbated in winter, when the climate is most unlike that which they are adapted to inhabit. However, the provision of heated indoor areas may allow the expression of necessary interactive behaviours in this highly social species, even when those behaviours are too energetically costly to be performed outside. By providing a space in which the ambient temperature is not so far

below their thermoneutral zone, zoos allow meerkats to perform social behaviours without compromising their thermoregulation.

In the wild, temperature and rainfall are closely correlated with foraging success (Doolan and Macdonald, 1996; English et al., 2012). Therefore, behavioural patterns are linked to annual seasonal changes. It is interesting to note that even when climate and food are unlinked, as is the case in zoos, meerkats' behaviour still changes with the seasons, although apparently more as a result of thermoregulation than food availability (Doolan and Macdonald, 1996; Habicher, 2009; Müller and Lojewski, 1986).

To conclude, the range and ratio of behaviours of zoo meerkats, although they differ from the wild, show similar patterns, with foraging taking up the most time in both situations. The provision of heated indoor areas is likely to allow meerkats to express the behaviours throughout the year which are necessary for the cohesion of their social system.

5 *Obesity in Zoo Meerkats*

5.1 Abstract

Obesity can cause health problems in zoo animals, but for many species the normal weights and rates of growth in the wild are unknown. Recent research on the growth patterns of wild meerkats in the Kalahari mean that it is now possible to assess how the weights of zoo meerkats compare to their wild counterparts, and what factors contributed to any differences. I collected the weights of 110 meerkats in nine zoos in the UK and Germany. Although there was a variation in weights between the zoos, in all cases the asymptote of the growth model which best fit the animals' weights was significantly heavier than the asymptotes seen in wild meerkats. 86.7% of the adult zoo meerkats were more than two standard deviations heavier than the average wild meerkat on at least one occasion, and therefore could be classified as obese. The difference between the expected weight of a wild meerkat and the observed weight of zoo meerkats was not affected by the activity level of the animal or its sex; however, those in larger enclosures tended to be heavier. This trend could not be explained by group size or the presence of pups, as these factors were found not to correlate with enclosure size. Meerkats were also found to be heavier in zoos which experienced higher rainfall and summer temperatures than in those in drier, cooler locations; this may be a result of the energy required for thermoregulation in colder climates. The fitness consequences of obesity in meerkats are unknown, but since it is so widespread it is important that zoos investigate the impact of weight on meerkats' general health in more detail.

5.2 Introduction

Zoo animals are commonly heavier than their wild conspecifics (Schwitzer and Kaumanns, 2001). Obesity is known to be a problem for some animals in zoos,

in particular primates (Schwitzer and Kaumanns, 2001; Terranova and Coffman, 1997; Videan et al., 2007) and large herbivores (Clauss et al., 2005; Harris et al., 2008). High weights have also been recorded in captive meerkats (Gutzmann et al., 2009). At the extreme end, obesity can have a negative effect on health: in the case of both Indian rhinoceros and Asian elephants, for example, it contributes to foot problems, which are a leading cause of euthanasia in the latter species (Clauss et al., 2005; Harris et al., 2008). In lemurs, female body weight is a factor in determining reproductive success, with obese lemurs failing to produce viable offspring (Terranova and Coffman, 1997). In humans, obesity is linked to cardiovascular disease, diabetes, arthritis, cancer and high blood pressure; similar risks have been identified in primate species (Videan et al., 2007).

The life history of animals in captivity differs fundamentally from that of their wild conspecifics in several ways which are relevant to size and growth (Terranova and Coffman, 1997), particularly in that food is provided for them (Hosey, 2005) and levels of activity which are typically much lower than their wild counterparts (see chapter 1 section 3 on comparing zoo and wild behavioural data). The body weight of an animal can be used as a proxy for its overall health and well-being, and as a method for monitoring the effect of husbandry changes (Terranova and Coffman, 1997). However, this requires a knowledge of ideal growth rates and asymptotic sizes for the target species, and for many species the size and growth rate which maximises health has not been established. Zoo animals are typically heavier than their wild counterparts, but for many species there is little information from the wild to assess whether or not animals are obese.

Meerkats *Suricata suricatta* provide a useful model species for assessing the impact of captivity on growth rates and asymptotic size because they are extremely well-studied in the wild. Meerkats are an obligate cooperatively-breeding species of mongoose which live in groups of two to 50 animals in dry regions of southern Africa (Clutton-Brock et al., 2008). A social group consists of a dominant male and female, which are the parents of the majority of pups born

in the group (Hodge et al., 2008), and both juvenile and adult helpers of both sexes, which participate in guarding and feeding the pups (Brotherton et al., 2001; Hodge et al., 2007). The group forages together in a loosely dispersed pattern, maintaining contact between group members by using contact calls (Townsend et al., 2010). Their diet consists primarily of invertebrates and small vertebrates, which are extracted from the ground in intensive bouts of digging in sand (Brotherton et al., 2001). Since all individuals in the group are foraging for the same prey, competition and possibly conflict might be expected, which would suggest that their growth is likely to be limited to less than that which they could achieve without competition for food. However, starvation is rarely observed as the primary cause of death in the wild, although poor condition linked to low food intake may be a contributing factor to deaths from predation and disease (S. Hodge, 2013, pers. comm.). English et al. (2012) analysed the weights of 162 wild meerkats over 12 years and assessed the suitability of a range of models to predict the growth patterns of individual animals. They found that a monomolecular model of growth most closely matched observed meerkat growth. The recorded weights of wild meerkats are fairly consistent across sources, with Kingdon (1997, p. 246) giving a weight of 620 to 970g, while Nel and Kok (1999) report that wild meerkats weigh up to 900g. An earlier study of the Kalahari Meerkat Project animals recorded mean (± standard error) weights adult meerkats of 721 ± 51g for dominant females, 640 ± 66.8g for subordinate females, 808 ± 86.1g for dominant males and 659 ± 69.5g for subordinate males (Clutton-Brock, MacColl et al., 1999), which compares to the mean asymptotic weight of 722.3g calculated by English et al. (2012). Published weights of zoo meerkats are substantially higher, with Gutzmann et al. (2009) reporting weights in the range of 1000 to 1500g, and the AZA zoo guidelines giving an expected weight range of 600 to 2500g (Kimble, 2003).

In zoos meerkats are commonly fed commercial animal foods, horse-meat, rodents, insects, fruit and vegetables, and their energy requirements are typically much lower than in the wild, with zoo meerkats maintaining their weight when their energy intake was less than half that of their wild conspecifics (Gutzmann et al., 2009). While keepers attempt to provide captive animals with

diets that resemble those of their wild counterparts, it is often difficult to ensure that captive individuals obtain sufficient but not excess food, given the constraints on their energetic expenditure. I have obtained information about the feeding regime of the meerkats for four of the nine zoos which are involved in this study. In these four zoos, the animals were fed between two and four times a day. They all received some live food (primarily mealworms and crickets), and most of their food was scatter-fed. Zoo pellets designed for carnivores were common, and most of the meerkats were given mixed fruit and vegetables. One zoo, Paignton, had analysed the diet their meerkats were receiving and found that it provided 81kcal per animal per day, which is lower than their estimate of 114kcal for a meerkat's daily energy requirement. However, given the large variations in methods of describing and measuring diets, and the likelihood that these diet sheets do not accurately represent the actual diets received by the animals, it was not possible to quantitatively compare the effects of diet on meerkats' weight, as had previously been done by Gutzman et al. (2009). This is an area which would benefit from further investigation.

English et al. (2012) also found that meerkat weights were influenced by time of year and recent rainfall. It was suggested that this was a result of both current food availability and the breeding cycle of the meerkats; it may also be, however, that body fat plays a role in thermoregulation for meerkats, and, therefore, animals exposed to cold weather, or high rainfall, as wet animals would be expected to lose body heat more quickly, and which have the option of building up fat storage might be expected to be heavier than those which only experience warm, dry conditions.

In this study I aimed to determine how meerkats in zoos compare in weight to their wild counterparts, and to assess what factors of captivity affect obesity. To assess the size and growth rates of captive meerkats, I collected weight data from animals of known age in nine zoos in the UK and Germany and compared it to published data on the weights of wild meerkats at the Kalahari Meerkat Project in South Africa. I tried to determine what factors of captivity influenced the difference in weights between wild and captive meerkats by assessing

correlations between weight and different factors of captivity: levels of activity and enclosure size.

5.3 Materials and Methods

Data were collected on 110 meerkats kept in nine zoos in the UK and Germany between 2005 and 2013, with between 1 and 55 measurements of each animal (mean: 7.82 measurements). The age of meerkats at weighing varied from 12 days to 3429 days old (mean: 778.0 days). Meerkats were weighed either by tempting them onto a set of scales or when unconscious for veterinary treatment. At three of the zoos measurement was performed by the authors with the assistance of zoo staff, while at the remaining zoos measurements were collected by zoo staff or other researchers and provided to the authors.

5.3.1 Monomolecular model for growth curves

English et al. (2012) found that a monomolecular model best fit the growth patterns of wild meerkats, so this same formula was used to model the growth and size of captive meerkats:

$$M_t = A\left(1 - \mathrm{e}^{-k\left(t - t_0\right)}\right)$$

Where mass (M) at time t is a function of the age at onset of growth (t_0), the growth rate constant (k) and asymptotic or final mass (A). A monomolecular model relates the rate of growth over time to the proportion of possible growth remaining, with the final mass A representing the maximum possible level of growth; it does not include an inflection point, so growth is fastest at the beginning of the time period and gradually slows (English et al., 2009). In this case the optimal values of A, k and t_0 were calculated for each individual animal, and the mean and standard deviation of these within each zoo is reported in

table 5.1.

The individual ID nested within Zoo was included as a random effect, and the mean value for all three coefficients from the meerkats in each zoo, and the standard deviation of individuals within the zoo, are included in the results.

English et al. (2012) identified seasonality and rainfall over the previous nine months as important factors in predicting the weight of an animal at a particular point in its life. Since meerkats in captivity in Western Europe experience a very different seasonal pattern to those in the wild, and as their food intake is not predicted by rainfall, the captive weights were compared to those of a wild animal experiencing the mean historic rainfall, and the seasonal sine-curve was removed.

Three meerkats in one zoo were excluded from this analysis, as there was not sufficient data to model.

5.3.2 Obesity in captive adult meerkats

A small sample of wild meerkats over the age of one year were weighed by Clutton-Brock et al. (1999) and the mean weights and standard errors of animals of each sex and dominance combination were calculated. In zoo meerkats, the dominance of individuals is not always clear, so an overall mean and standard error for wild meerkats of each sex was calculated using the formulae:

$$mean = \frac{\overline{X} * n_x + \overline{Y} * n_y}{n_x + n_y}$$

$$standarderror = \sqrt{\frac{n_x^2 s_x^2 + n_y^2 s_y^2 - n_y s_x^2 - n_y s_y^2 - n_x s_x^2 - n_x s_y^2 + n_y n_x s_x^2 + n_y n_x s_y^2 + n_y n_x \left(\overline{X} - \overline{Y}\right)}{\left(n_x + n_y - 1\right)\left(n_x + n_y\right)}}$$

where *x* represents the dominants in the wild sample and *y* represents the subordinates, *s* is the standard error, *n* is the sample size and *X* and *Y* are the sample means (Headrick, 2010, p. 137). This gave a mean weight (± standard error) for wild females (n=15) of 672.4g ± 67.2g and for wild males (n=21) of 722.9g ± 101.5g. The mean and standard error of all the animals could also be calculated using the above equations to combine males and females, which gave a mean overall weight (± standard error) of 701.8g ± 88.8g (n=36). Using the definition of obese as when an animal weighs more than two standard deviations more than the mean wild weight (Schwitzer and Kaumanns, 2001; Terranova and Coffman, 1997), we can identify obese adult meerkats in zoos as those which are over a year old and heavier than 806.9g if female, or 925.8g if male. All animals of this age were of known sex.

5.3.3 Other factors that could affect weight

To assess the importance of other factors on meerkats' weight, I used the difference between observed weights and those predicted for an average meerkat by the monomolecular model of English et al. (2012) as a proportion of predicted weight, to account for lower variation around lower values. This metric, proportional difference in weight from model, was used as the response variable in general linear mixed models, with individual ID nested within zoo as random effects. The fixed effects considered were sex, enclosure size, activity level, and the interaction between the latter two factors; age was included to make sure that the response variable in use took growth sufficiently into account. It was not possible to include dominance status in the analysis as in many cases this data was not available.

Enclosure size was defined as the total floor area, outdoor and indoor, which the meerkats had access to during the day. Data on this was available for 84 of the 110 meerkats, accounting for 472 of the 815 observations.

Behavioural data was collected on 37 of the 110 meerkats included in this study. Scan samples recording the behaviour and location of each animal in the social group were performed every two minutes for twenty minutes, followed by a break of twenty minutes or more. Between 25 and 62 of these 20-minute sessions were performed for each animal (see chapter 3 on behaviour for more details). Activity level was calculated by dividing the number of times each animal was recorded performing an active behaviour (running, walking, foraging, play-fighting or digging) by the number of times it was recorded as passive (sitting, huddling or sunbathing).

Weights were only included if the enclosure size, activity level and sex were known. This gave a total of 169 measurements of 32 meerkats in six zoos.

Information about the size of the social group in which the meerkat was kept was not available for every weight. However, it was hypothesised that group size could be linked to enclosure size, and so, for nine zoos which had been visited, containing eleven groups of meerkats, an analysis was performed to assess the correlation between enclosure size and both group size and presence of pups on that occasion. For groups which had been visited more than once, the mean group size was used. This analysis included information on four groups of meerkats for which weights were not available.

To analyse the effect of climate on captive meerkats, data on highest mean monthly maximum temperature, lowest mean monthly minimum temperature and annual days of rain were collected for the nearest major city to each zoo from the World Meteorological Organization (World Meteorological Organization, n.d.). This data was modelled against the proportional difference between observed and expected weights. To check that this model was not too heavily influenced by the data from the zoos which measure their meerkats most regularly, the climate metrics were also modelled against a single value for each zoo: the asymptote (A) calculated from the monomolecular growth curve.

Statistical analyses were performed in R 3.0.1 (R Development Core Team, 2013).

5.4 Results

5.4.1 Monomolecular model for growth curves

Using the monomolecular formula identified by English et al. (2012) as the most representative monophasic measure of meerkat growth, I calculated the values of the variables A, k and t_0 which most accurately reflected the distribution of weights of captive meerkats, with individual nested within zoo as random effects. The results are presented in Table 5.1.

Table 5.1: The average value for variables A, k and t_0 for all individuals within each zoo, with the standard deviation of variables also indicated.

	Number of:		Mean and standard deviation of value for individuals in each zoo		
	Animals	Observ-ations	A	k	t_0
Kalahari meerkats[1]	162	~66900	722.3 ± 7.7	not available	-5.3 ± 1.7
Bristol Zoo	12	29	983.8 ± 40.7	0.00313 ± 0.00149	-15.5 ± 0.1
Chester Zoo	10	10	1097.9 ± 16.7	0.00398 ± 0.00068	-7.7 ± 0.1
Cologne Zoo	21	265	1381.0 ± 98.5	0.00547 ± 0.00072	9.7 ± 0.2
Longleat Safari Park	14	97	1106.8 ± 120.7	0.00654 ± 0.00253	-0.0 ± 0.3
Newquay Zoo	5	5	986.2 ± 17.8	0.00361 ± 0.00060	-13.4 ± 0.1
Paignton Zoo	3	44	863.6 ± 66.2	0.00371 ± 0.00026	-17.7 ± 0.2
Shaldon Wildlife Park	5	5	802.9 ± 40.2	0.00427 ± 0.00005	-19.2 ± 0.1
ZSL	32	343	1038.9 ± 99.6	0.00786 ± 0.00098	2.7 ± 0.2

[1]from English et al. (2012)

The asymptote *A* is significantly higher for all zoos than would be expected if the populations were drawn from the same pool as the wild data (unmatched t-test, test statistics shown in table 5.2). The 95% confidence interval for the actual difference in asymptote between the wild population and each zoo is shown in table 5.2.

Table 5.2: The difference between the asymptotic weights (A) of meerkats in each zoo, compared to wild meerkats (data from English et al., 2012) with 95% confidence intervals for the actual difference between average asymptotes

				95% confidence interval (g)	
	t-value	Degrees of freedom	p-value	Lower limit	Upper limit
Bristol Zoo	68.8	172	<0.001	254.0	269.0
Chester Zoo	136.9	170	<0.001	370.2	381.0
Cologne Zoo	84.7	181	<0.001	643.5	673.9
Longleat Safari Park	40.8	174	<0.001	366.0	403.0
Newquay Zoo	71.8	165	<0.001	256.7	271.1
Paignton Zoo	22.9	163	<0.001	129.2	153.4
Shaldon Wildlife Park	18.0	165	<0.001	71.8	89.4
ZSL	40.3	192	<0.001	301.2	332.0

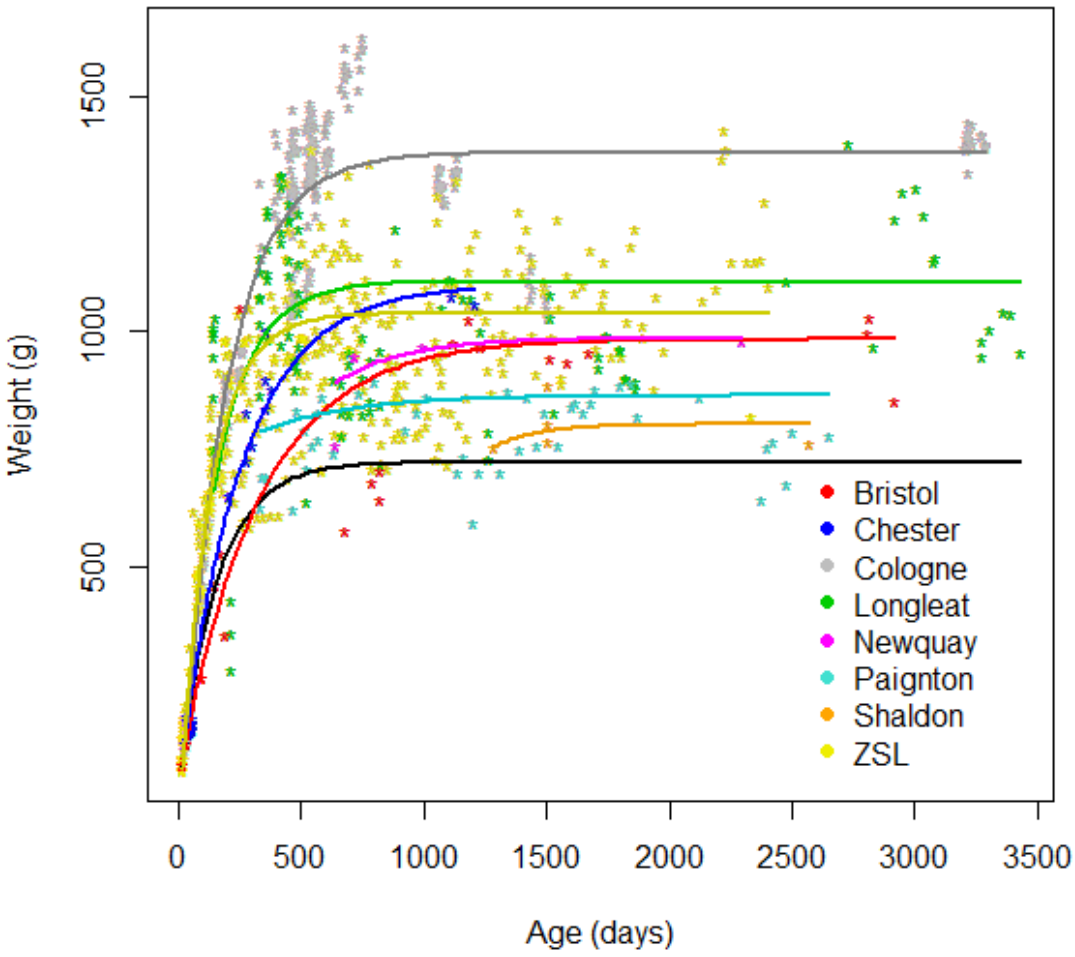

Figure 5.1: Plot of weight of captive meerkats in grams against their age in days at eight European zoos, with lines showing the model predictions which most closely fit the data from each institution, plus the model of growth of an average wild meerkats described in English et al. (2012) in black.

5.4.2 Obesity in captive adult meerkats

Of the 75 meerkats from nine zoos in the captive sample which were weighed at 366 days or older, 56 (74.7%) weighed more than 925.8g (for males) or 806.9g (for females) every time they were weighed; 9 animals (12.0%) weighed more than this at least one of the times they were measured but on other occasions

were below that level, and 10 (13.3%) were never found to be above this weight. In total, 86.7% of full-grown meerkats weighed were recorded at least once as more than two standard deviations heavier than the mean of their wild conspecifics (see figure 2). The mean weight of these captive adult meerkats was 1038g. This is lower than the body weights found in a previous study on meerkats in American zoos (Gutzmann et al., 2009).

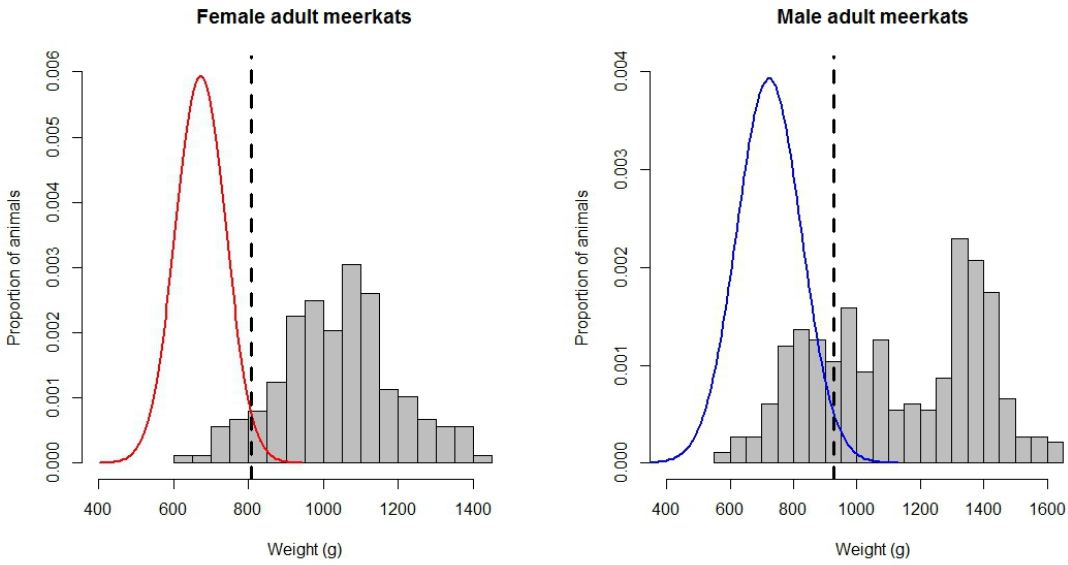

Figure 5.2: Histograms of weights of female (left) and male (right) adult meerkats in zoos, with bell curves showing the distribution of weights of wild meerkats reported by Clutton-Brock, MacColl et al. (1999). The vertical black lines mark two standard deviations above the mean weight of wild meerkats.

5.4.3 Other factors that could affect weight

Using the difference between observed weights and those predicted by the monomolecular model of English et al. (2012) as a proportion of predicted weight, age is not a significant factor in predicting this value, indicating that this metric accurately take growth into account (general linear mixed model with individual nested within zoo as random effects, χ^2_1=1.70, p=0.192); nor is sex a significant predictor of weight (general linear mixed model with individual nested within zoo as random effects, χ^2_1=1.43, p=0.232). The ratio of time spent active

to time spent inactive is not a significant predictor of weight either (general linear mixed model with individual nested within zoo as random effects, χ^2_1=1.88, p=0.170). Captive meerkats are further above their expected weight when kept in large enclosures (general linear mixed model with individual nested within zoo as random effects, χ^2_1=8.02, p=0.005, see figure 5.3). This analysis included only the 169 occasions on which animals were weighed when their sex, enclosure size and activity level were know. The analysis of the effect of enclosure size was repeated including all weights of animals in enclosures of known size, and the result was qualitatively identical (general linear mixed model with individual nested within zoo as random effects, χ^2_1=13.93, p<0.001).

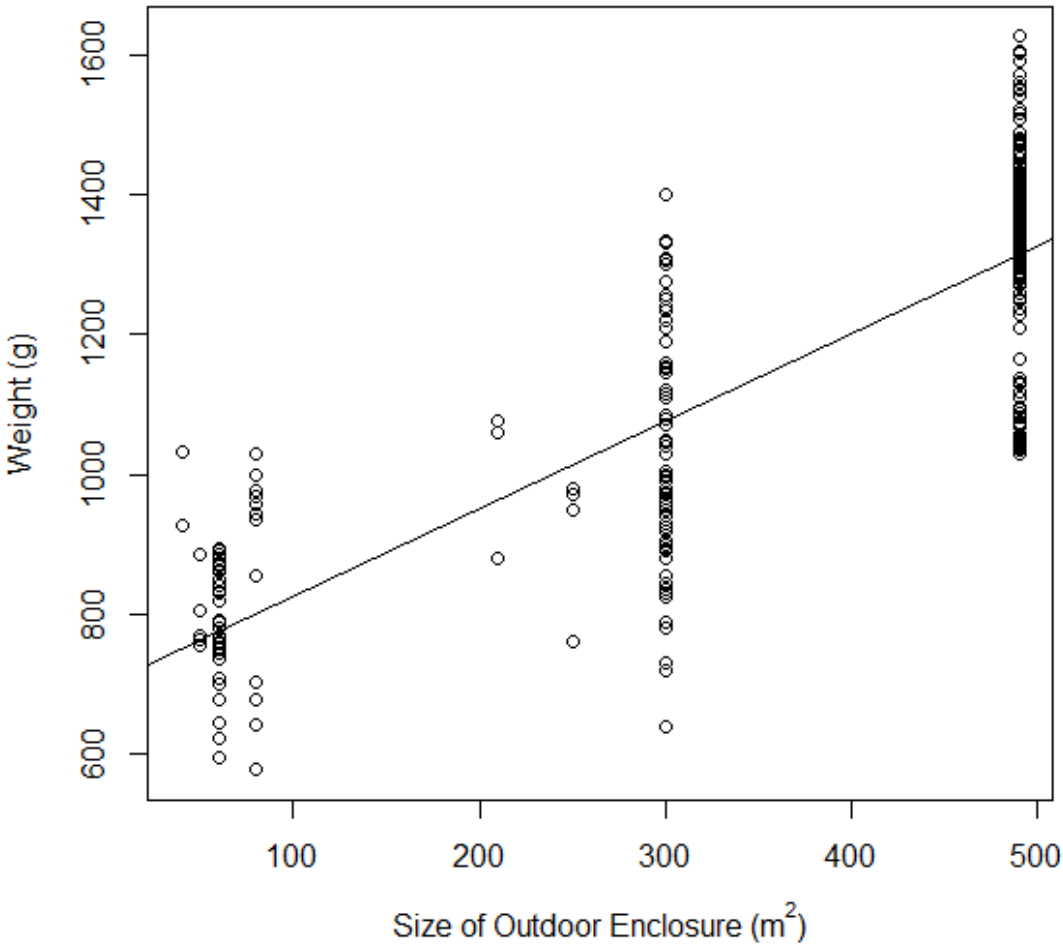

Figure 5.3: Mass of adult meerkats in grams against size of enclosure in square metres. In this graph only full-grown meerkats (those over 365 days old) are included.

As weight data was collected over several years, and group sizes change regularly, it was not possible to assess if there was a correlation between group size and weight. However, analyses of point observations of enclosure size, group size and presence of pups in eleven groups at nine zoos show that enclosure size is not correlated with group size (general linear model, $F_{1,9}$=1.24, p=0.294) nor with presence of pups (general linear model, $F_{1,9}$=1.77, p=0.216), nor was there an interaction between the two factors (general linear model, $F_{1,7}$=0.770, p=0.409). Interestingly, presence of pups was not found to be linked to group size either (general linear model, $F_{1,9}$=0.554, p=0.476). This is likely to

be because, in most cases, the lack of current breeding success can be linked to unsuitable group structures – for example, bachelor groups or high relatedness between adults. The influence of group size on pup survival in the wild is not conclusive. Russell et al. (2002) found that pup survival from weaning to independence was positively related to group size in groups of up to 19 animals, and then negatively related to larger group sizes. However, Clutton-Brock et al. (1998) found the probability of pups' survival did not vary with group size, with each helper taking on more of the babysitting in smaller groups.

When proportional difference between observed and expected weights was modelled against climate metrics, it was found that in locations with a higher average annual number of days of rain, meerkats weighed more than in drier places (general linear mixed model with individual nested within zoo as random effects, $\chi^2_1=4.15$, p=0.042). Likewise, zoos which experienced a higher average daily maximum temperature in the hottest month of the year had heavier meerkats than those in cooler locations (general linear mixed model with individual nested within zoo as random effects, $\chi^2_1=7.54$, p=0.006). The average daily minimum temperature in the coldest month (general linear mixed model with individual nested within zoo as random effects, $\chi^2_1=0.316$, p=0.574) was not significant. The same climate metrics were also modelled against the asymptote (*A*) calculated for each zoo using the monomolecular growth model, and again days of rain and highest average maximum temperature were both positively correlated with proportional difference between observed and expected weight (rain days: general linear model, $F_{1,5}=15.0$, p=0.012; highest average maximum temperature: general linear model, $F_{1,5}=16.4$, p=0.010). Lowest average minimum temperature was once again not significant (general linear model, $F_{1,4}=0.133$, p=0.734).

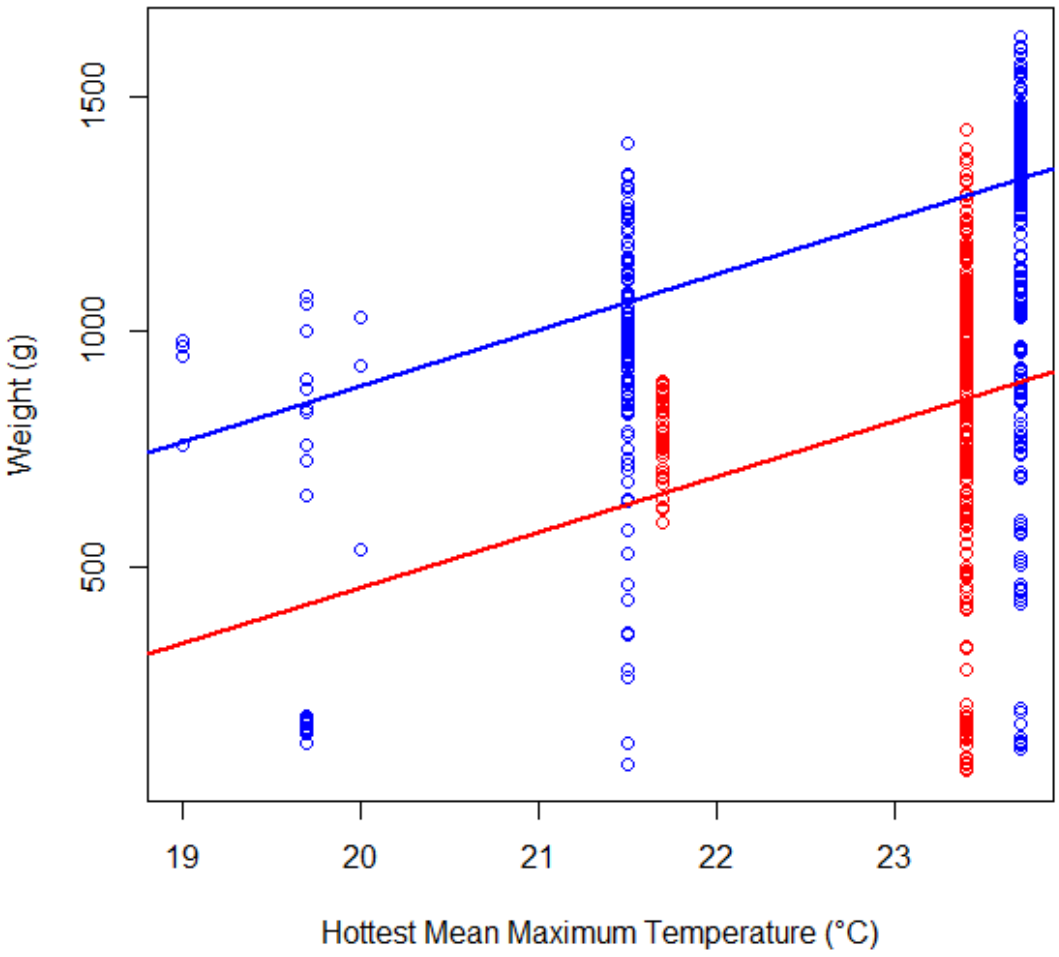

Figure 5.4: Mass of adult meerkats in grams against highest maximum mean monthly temperature in degrees centigrade. The mean number of annual days of rain was 121.7. Zoos with below-average number of rain days are indicated in blue, and above-average in red. The lines indicate the model of effect of temperature on body weight in the driest (red) and wettest (blue) locations.

5.5 Discussion

The data collected and analysed in this study show that captive meerkats are
2495 generally heavier, often much heavier, than their wild conspecifics in the Kalahari. While rates of growth vary between zoos, the mean final adult weight

achieved is universally higher than that seen in the wild. Of the adult meerkats weighed, 86.7% were found to be more than two standard deviations heavier than the wild mean on at least one occasion. Weights of males and females were not found to differ significantly, and weight did not correlate with activity level. However, animals in larger enclosures were heavier than those in smaller enclosures; this could not be explained by an effect of group size or the presence of pups, as neither of these factors correlated with enclosure size. Weather seemed to be related to meerkat weight, with heavier meerkats in zoos with high rainfall and high summer temperatures.

There are a number of possible reasons for the weight difference between wild and captive meerkats, and it has not been possible in this analysis to determine which, if any, are valid. It may be partly due to a more nutritional diet allowing animals to reach their full growth potential (Schwitzer & Kaumanns, 2001). It could also be the case that the meerkats examined in this study are from a different sub-population or even subspecies from the Kalahari Meerkat Project animals, and are genetically predisposed towards heavier body size. However, weights reported for wild meerkats, even outside the Kalahari Meerkat Project population, are consistent with the weights reported by English et al. (2012) (Kingdon, 1997; Nel and Kok, 1999). It has not been possible to measure the size of any captive meerkats, for comparison against individuals in the wild population, which would have allowed an analysis of weight relative to body size, so that an estimate could be made of the difference in body fat content. This ideally would be a channel of future research. However, working with the information available, and using accepted metrics of obesity, this research suggests that excess weight in captive meerkats is a serious problem of which zoos should be aware.

It was not possible to investigate the effect of diet on captive meerkat weights in this study, but this is certainly an area which would benefit from more detailed research. Gutzman et al. (2009) were able to reduce the weights of zoo meerkats by regulating their diet, as might be expected. Of the nine zoo groups in the current study, the calorific content of only one of the groups' diet was

know, and this was a reducing diet which provided fewer calories than were estimated to be used daily. This group had one of the lowest asymptotic values of all the zoo groups, suggesting that the low-calorie diet is effective in preventing high weights. In addition, at another zoo, Longleat, I was told by keepers that the animals had been put on a reducing diet at a particular point in time, and the meerkats' weights generally decreased after that point. These pieces of anecdotal evidence suggest that diet has an important role to play in controlling the weights of zoo meerkats.

The weight-based definition of obesity which I use was originally developed from physical examination of Rhesus monkeys, but has been applied to a wider range of species (Kemnitz et al., 1989; Terranova and Coffman, 1997). However it does make several assumptions which may not be justified in meerkats, specifically that weight correlates with fat deposits, and that these have direct consequences for health. The relationship between weight and fat deposits has not been examined in many species, but body weight is a significant predictor of obesity in female chimpanzees (Videan et al., 2007). Whether this holds true for meerkats could be tested by post-mortem examination of fat deposits in captive meerkats, which would provide validation for this metric.

The analysis of correlation of weight to aspects of captivity showed that animals kept in larger enclosures tended to be more overweight than those in smaller enclosures. This is contrary to expectations, as it was hypothesised that animals with more space to move would use up more energy and so be less heavy. However, it was also shown that the amount of activity an animal habitually performs is not correlated with its weight. The enclosure size effect may therefore be an indication of some other aspect of the animals' environment. Animals in larger, naturalistic housing may increase their food intake because they have more opportunities for natural foraging (Terranova and Coffman, 1997). Alternatively, even if overall activity is unaffected it may be that large enclosures encourage animals to travel further or to undertake more strenuous activity, developing more muscle mass (Terranova and Coffman, 1997). As described, it was not possible in this study to distinguish from weights

data how much of that weight is due to fat and how much to muscle. Nor was it possible to include group size in this analysis as it changed too often, so that the exact group size on each day of weighing was often unknown. I hypothesised that larger groups might be kept in larger enclosures, and so the observed enclosure size effect could in fact be a result of group size. In pigs, both group size and population density have significant negative effects on weight gain, although enclosure size does not have an effect (Estevez et al., 2007; Turner et al., 2000). Similarly, in broiler chickens, high density was found to reduce bodyweight (Estevez et al., 2007); but the densities in which farmed chickens and pigs are kept are orders of magnitude greater than those which captive meerkats experience. Behaviourally, the expected effect of being in a large group is unclear: with many companions, an individual need spend less time in energetically costly cooperative behaviours such as babysitting, pup feeding and burrow maintenance; it may also lose less energy in thermoregulation, particularly at night. However, more individuals means more animals to compete with for food. In the wild, this might be expected to have a significant effect, but in zoos animals living in social groups tend, if anything, to be fed to excess to ensure that even the lowest-ranking individual can access sufficient food (Schwitzer and Kaumanns, 2001). This trend is likely to be more pronounced the larger the group is, so in a large group each animal would have access to more food and thus be heavier. Our analyses indicated that there was not a significant correlation between enclosure size and group size, so while the size of social group might have an effect on meerkats' weights, it does not explain the observed enclosure size effect.

The hypothesis that captive meerkat weight may be linked to the climate they experience seems to be supported by the results reported, with warmer, wetter places having the heaviest meerkats. The direction of the effect is surprising, because I hypothesised that meerkats would build up greater fat reserves to combat colder weather. However, it could be that since they use up less energy in thermoregulation in a warmer climate, they are therefore able to convert more of their food into fat and body tissue. Another climatic effect is that adaptation to the strongly seasonal environment of southern African desert might predispose

meerkats, when kept in a situation of stable food supply, to gain weight, as is observed in captive lemurs (Schwitzer and Kaumanns, 2001). For further discussion of the effect of climate and weather on captive meerkats, see chapter 4, where I conclude that captive meerkats experiencing climates unlike those in which they evolved use thermoregulatory behaviours to regulate their temperature, and take advantage of artificial shelter to perform social and interactive behaviours.

The consequences of excess weight in captive meerkats are unclear. In the wild, high weight has been associated with probability of becoming dominant in females (Clutton-Brock et al., 2006; Hodge et al., 2008) and the difference in weight between the dominant female and the heaviest subordinate correlates positively with the length of tenure of the dominant (Clutton-Brock et al., 2006). In addition, body weight in females is associated with the individual's level of contribution to cooperation (Carlson, Russell et al., 2006; Clutton-Brock et al., 2002). Whether these effects on behaviour hold true in a captive population with sufficient food and no ability to emigrate into neighbouring social groups is undetermined, but this would be a useful direction for future research.

In many species, obesity of captive animals has been linked to health problems. Currently, the effect of obesity on meerkats' health is unknown, but this study shows how widespread this problem is, with 86.7% of adult meerkats recorded as being more than two standard deviations heavier than their wild counterparts. To determine the effects of this, further investigation into the veterinary records would be required. However, it can be concluded that with so many heavy meerkats, it behoves zoos to examine the health of their animals closely. Systematic weighing of captive individuals should be encouraged as part of the assessment of their physical well-being, and as an important measurement for informing husbandry decisions (Terranova and Coffman, 1997).

6 Hormonal Stress in Zoo Meerkats

6.1 Abstract

Measuring hormonal stress in zoo animals can give important insights into how they are affected by the captive environment. I analysed the levels of glucocorticoid metabolites in faecal samples from zoo meerkats as a proxy for blood cortisol concentration, high levels of which are associated with a stress response. The levels of faecal glucocorticoid metabolites (fGCs) that I found in samples from captive meerkats were lower than those previously reported for their wild counterparts; this may be because they perceive their environment to be less stressful, but it may also be a consequence of their different nutritional regimes. In the wild, studies have shown both positive and negative correlations between cortisol levels and group size; in zoo meerkats I found that animals in larger groups had lower levels of fGCs, which supports the hypothesis that their is an optimum group size which minimises hormonal stress. In the wild, very small groups of meerkats are at a higher risk of predation, while in very large groups there is increased competition for resources. The sex, age, dominance status, enclosure size, breeding status, season and meerkat density were not found to have significant effects on fGCs. The number of visitors did affect the fGC levels of captive meerkats: the highest fGCs occur when the median number of visitors is high but the maximum is low, while the lowest fGCs are found when the median number of visitors is low but there are large spikes in visitor numbers. Therefore the zoo meerkats most at risk of high levels of hormonal stress are those which experience generally high levels of zoo visitors but without large peaks, and which are kept in small groups.

6.2 Introduction

Measuring stress in zoo animals is important to assess welfare and monitor the

effect of captivity, but is difficult in practice. Variation between species and between individual animals in their behavioural responses to a stressor make it extremely difficult to define fixed, reliable physical cues for identification of welfare-reducing conditions (Busch & Hayward, 2009; Creel, 2001). There are observational measures which can provide useful information, such as breeding success, behavioural repertoire, or morphological state (Melfi, 2009). However, a particularly illuminating method is to gain an insight into the animal's internal systems which govern the physical response to an external stressor via a stress response.

The hormone associated with coordinating the stress response in most mammals is cortisol, a member of the glucocortiocoid family of molecules, which is released into the blood stream from the adrenal gland and triggers the mobilisation of energy stores to allow the animal to respond to the current threat (Creel, 2001; Santema et al., 2013; Young, K.M. et al., 2004). Cortisol plays an essential role in general homeostasis, but its presence at a concentration elevated above an animal's baseline level can also indicate a stress response. Thus, analysing the level of cortisol in the animal's bloodstream is a way to measure the level of the hormonal stress response at a given time. However, this requires catching than animal and extracting a blood sample: this is impractical in zoos, and capture itself constitutes a stressor which will compromise future samples for as long as the stress response lasts, and possibly even longer if a stressor results in longer term changes in an animal's state (Schwarzenberger, 2007; Young, K.M. et al., 2004). An alternative method is to analyse the level of cortisol's metabolites in a faecal sample from the animal. Depending on rate of metabolism and volume of through-put, this can give an estimate for the average level of glucorticoids – mainly cortisol – in the animal's blood stream over the preceding hours or days. For the same animal, or conspecifics on similar diets, this provides a relative measure of hormonal stress response above the baseline cortisol level at different times or in different situations. Using faecal sampling to monitor glucocorticoid levels has become a widespread technique over recent years (for references see Schwarzenberger, 2007).

When studying the glucocorticoid response of zoo animals and the effect of the surroundings they are kept in, their social group, and their individual characteristics, it is particularly useful to be able to compare these to wild conspecifics to assess whether conditions experienced solely by captive animals are affecting their cortisol levels, and thus how captivity affects stress. In this way studies of captive and wild animals can complement each other. In this study I used meerkats (*Suricata suricatta*) as a model to examine the effect of captivity on the stress-response of a highly social and cooperatively-breeding species. Meerkats have been extensively studied in the wild, with the effects on their behaviour of natural variation in cortisol levels well documented, and are also common in zoos, allowing a relatively large sample size of varying individuals in different social and environmental conditions to be studied.

Meerkats are an obligate cooperatively-breeding species of mongoose which live in groups of two to 50 animals in dry regions of southern Africa (Clutton-Brock et al., 2008). A social group consists of a dominant male and female, which are the parents of the majority of pups born in the group (Hodge et al., 2008), and both juvenile and adult helpers of both sexes, which participate in guarding and feeding the pups (Brotherton et al., 2001; Hodge et al., 2007). Their diet consists primarily of invertebrates and small vertebrates, which are extracted from the ground in intensive bouts of digging in sand (Brotherton et al., 2001). Glucocorticoids have been linked in wild meerkats to behaviours which are very important to a social species, including babysitting, pup feeding, dispersal away from the group by males, and repression of reproduction in subordinate females (Carlson, Manser et al., 2006; Carlson, Russell et al., 2006; Young, A.J. and Monfort, 2009; Young, A.J. et al., 2006). Contribution to the cooperative behaviour of pup feeding has been shown to be positively correlated with plasma cortisol levels, which are elevated by pup begging calls (Carlson, Manser et al., 2006), but a lower level of cortisol was seen immediately before a meerkat's decision to babysit (Carlson, Russell et al., 2006), demonstrating cortisol's complex influence on cooperative behaviours. In the wild, meerkats which are on their own, such as evicted females or roving males, have a much higher level of faecal glucocorticoid metabolites (fGCs)

than those within a group, probably due to higher predation threat (Young, A.J. and Monfort, 2009; Young, A.J. et al., 2006). As group size increases, the risk of predation or attack from other meerkat groups decreases, as does the proportion of cooperative behaviours, such as sentinel duty and pup feeding, which are performed by each individual (Carlson, Manser et al., 2006; Clutton-Brock, Gaynor et al., 1999). I expect therefore that hormonal stress would be lower in animals in larger groups. On the other hand, as groups get bigger, more conflict would be expected between individuals within the group, such that beyond a certain group size the hormonal stress levels may start to rise again (Clutton-Brock et al., 2008). The effect of group size on faecal glucocorticoids has been investigated in the wild: Santema (2013) found that, in groups of three to 32 animals aged 90 day or older, there was a weak positive correlation between group size and fGC concentration; however, Young (2003) measured fGC in dispersing coalitions in the wild – containing numbers of meerkats more similar to those in captive groups – and found a negative relationship between group size and fGC level. It could be that this contradiction is a result of different ranges of group size. Santema (2013) looked at groups ranging from three to 32 individuals, with a median of 15, while Young (2003) studied coalitions of one to ten animals, with a mean of 2.93. The contrasting effects could be explained if there was an optimum group size of around eight individuals which minimised fGC, and any variation away from this in either direction resulted in fGC increasing. On the other hand, it could be that single-sex dispersing groups have a fundamentally different hormonal response to group size. Specifically, in stable mixed-sex groups hormonal stress would be lower if there are fewer animals, but in dispersing coalitions the opposite would be true.

In this study I examine meerkats in stable, mostly mixed-sex groups, but the range of group sizes more closely resembles those of dispersing coalitions. If, therefore, fGC in zoo meerkats has a negative relationship with group size it would support the former hypothesis, of an optimum group size, while if the relationship between fGC and group size is positive it would support the latter hypothesis, of a fundamental hormonal difference between stable and dispersing groups. Differences in stress responses between dominance ranks,

and between sexes, might be expected as dominant animals struggle to maintain their reproductive monopoly (Young, A.J., et al., 2008a); variation might also be expected depending on time of year, as temperature and weather have been reported to affect circulating glucocorticoid levels in other mammals (Beehner and McCann, 2008), and the point in the breeding cycle. In the wild, foraging success is likely to be important in determining fGC levels, as less food will lead to both a need to mobilise energy stores and a lower through-put, resulting in higher fGCs; high blood cortisol in turn stimulates higher foraging rates (Koch et al., 2002). In captivity, this is unlikely to be a major factor as enough food is provided for each animal to fulfil their nutritional requirements. In addition, competition with other groups of conspecifics and predation are negligible or non-existent in captivity, but it may be the perceived rather than the actual threat of these factors which determines fGC concentration, and these may differ greatly.

Our aim here is to test whether a) individual attributes (sex, age and dominance), b) group level attributes (group size, enclosure size, space per meerkat, season and presence of pups), and c) the presence and number of visitors, correlate with the concentration of glucocorticoid metabolites found in the meerkat's faeces. I will also assess the differences in fGC concentration between captive and wild meerkats, although with the caveat that, because of the significant differences in diet between these two populations, direct comparisons must be regarded with caution.

6.3 Materials and Methods

6.3.1 Sample collection

In total, 140 faecal samples were collected from meerkats in 10 different social groups at eight zoos in England. In summer 2011, 48 samples, mostly of unknown origin, were collected daily from four social groups. A further 21

samples from the same groups were collected in winter 2011/12. In summer 2012, 40 one-off samples were collected from mostly known individuals in six social groups, using a glitter-feeding technique developed by Marta Manser and colleagues at the University of Zürich; this was repeated in winter 2012/13, with 31 samples collected from animals in five zoos. The glitter-feeding method used to identify the origin of each sample had previously been found not to be harmful in meerkats (Manser and Gonçalves, pers. comm.), but to prevent any possibility of a build-up of glitter in the animal's digestive tract it was only performed once in each six-month period. Briefly, a small quantity of food taken from the animal's daily diet – ranging from banana slices or grapes to horse meat or chicken – was coated in very fine embossing glitter. Each piece of food had a different colour of glitter on it, and each was given to a different meerkat, identified either visually or from its microchip. Food pieces were small, and used food with which the animal was familiar, to reduce the risk of the selected animal rejecting it. However, the meerkats were watched to determine in each case whether the target animal consumed its piece, and if not the food was either removed or the animal which did eat it was identified. Faecal samples were collected during the following 36 hours and the presence and colour of the glitter they contained identified on site before freezing. All samples were stored at -70ºC for between five and 87 weeks before being transferred, frozen, to the Heistermann Endocrinology Laboratory at the German Primate Centre in Göttingen.

Based on the appearance of glitter in the faeces after glitter-feeding, through-put rate in captive meerkats appears to be between 12 and 36 hours; faecal glucocorticoid metabolites would therefore represent the animal's blood cortisol levels over the previous 24 hours or so. This accords with the findings of other researchers (Manser and Gonçalves, pers. comm.).

Faecal glucocorticoid metabolite (fGC) concentrations were analysed using a corticosterone enzyme immunoassay, using the antibody which was established to monitor meerkat fGC by Young et al. (2003; 2006) in a radioimmunoassay. Extraction was performed following previously described methodologies

(Heistermann et al., 2004). To outline the procedure: the samples were freeze dried at -20ºC, then pulverised and sieved to remove coarse material. At this stage, any obvious physical qualities of the samples were noted, such as the presence of large quantities fur or feathers in the faeces (which was thought to result from the animals having been fed chicks the previous day), or substantial amounts of sand coating the sample, due to the substrate from which the faeces were collected. As much extraneous sand was removed as possible. Between 0.0900g and 0.1100g of each sample was weighed out and the weight recorded to four decimal places. 3ml of 80% methanol was added to each sample, then they were shaken for 10min in a vortex and centrifuged at 3000rpm for 10min. 2ml of supernatant from each sample was decanted into eppendorfs for the glucocorticoid assay, and stored at -20°C until hormone analysis.

Faecal extracts were diluted 1:10 (except 3 samples with very low levels of fGCs that were diluted 1:3 and 1 sample with very high levels of fGCs that was diluted 1:100) in assay buffer (0.04M PBS, pH 7.2) and duplicate 50µl aliquots were measured by microtiterplate EIA along with 50µl aliquots of reference standard in doubling dilutions over the range of 1.9-125pg (Heistermann et al., 2006). The plates were incubated overnight at 4°C, then washed three times and incubated with 150µl streptavidin–peroxidase (HRP) for 30min in the dark at room temperature. Following a second washing step, 150µl of HRP-substrate solution was added to each well. After 45min of substrate incubation the enzyme reaction was stopped with 50µl 2M H_2SO_4 to each well. Absorbance was measured at 450nm (reference 630nm) on a plate reader. Sensitivity of the assay was 1.9pg. Specificity data (cross-reactivities) of the assay are reported in Heistermann et al. (2006). Intra-assay coefficients of variation for low and high value quality controls were 5.9% (n=16) and 7.9% (n=16), respectively. Respective figures for inter-assay CV values were 8.1% (n=10) and 11.4%. (n=10). All fGC levels reported are expressed as ng/g dry faecal mass.

6.3.2 Data analysis

Date were analysed using R 3.0.1 (R Development Core Team, 2013). A normalising base-10 logarithm was applied to the glucocorticoid concentration data. To assess the effect of the factors which vary between individuals, age, sex and dominance status, I included only the samples which were from known individuals. As none of these factors were significant, I was able to use all samples when considering the fixed effects group size, area of outdoor enclosure, population density, season, the presence or absence of pups, and the condition of the sample. I also investigated the effect of visitor number, using the mean, median and maximum number of visitors observed on the day of sample collection and on the previous day. In all three cases, a General Linear Mixed Model including all the fixed effects was built, with the animal's identity nested within social group as random effects, and model simplification applied, removing the least significant available term at each stage.

6.4 Results

A total of 140 meerkat faecal samples were analysed during the lab visit, of which 17 were found to contain glucocorticoid levels below the assay sensitivity threshold. Since an actual glucocorticoid concentration of zero is unlikely, these were included in the analysis at the minimum assay sensitivity of 2.28ng/g faeces, based on a sample weight of 0.1000g and a dilution of 3 (the lowest dilution used). The GC levels in the remaining 123 samples varied between 7.34 and 2299.80 ng/g faeces, with a mean of 100.34 ng/g faeces and a median of 58.37ng/g faeces; this difference in averages was due to a single outlier which was five times greater than the next highest value (marked in red on figure 6.1).

6.4.1 Individual-level factors

For 59 of the 140 samples it was possible to identify the individual animal from which it came. These 59 samples were used to investigate the effect of sex, dominance and age on the level of faecal glucocorticoid metabolites. All of these factors were included in the full model, along with all interactions between them, and the number of animals in the group. Individual ID nested within zoo were included as random effects, to account for multiple samples being collected from the same individual. The results are show in table 6.2. The level of glucocorticoid metabolites in meerkats' faeces decreased in an exponential pattern as group size increased. The sex of the animal, its age, its dominance status, and the interactions between these variables did not have a significant effect on faecal glucocorticoid concentration.

Table 6.1: General Linear Mixed Model of individual factors affecting the level of glucocorticoid metabolites in meerkat faeces. This analysis was based on a data set of 59 faecal samples from 31 animals in 10 social groups. The minimal adequate model, excluding random effects, explained 12.8% of the variation.

Full Model	**Chi squared**	**d.f.**	**P**
Age:Sex:Dominance	3.21	1	0.0734
Age:Dominance	0.185	1	0.667
Age:Sex	<0.001	1	0.982
Sex:Dominance	<0.001	1	>0.999
Group Size	4.29	1	**0.0383**
Sex	0.520	1	0.471
Age	0.409	1	0.523
Dominance	0.248	1	0.619
Minimum adequate model	**Mean effect**	**Standard error**	
Intercept	4.30	0.492	
Group Size	-0.111	0.0510	
Random effects	**Variance**	**Standard deviation**	**Number of levels**
ID:Zoo	0.417	0.645	31
Zoo	0.242	0.492	10
Residual	1.52	1.23	

6.4.2 Group-level factors

Since age, sex and dominance did not seem to have an effect of fGC concentration, all 140 samples were included in the analysis of group-level effects. Factors included were group size, the total available outdoor space, density (group size divided by enclosure size in m^2), the season (summer or

winter), whether or not there were pups present, and the condition of the sample (whether it contained a large amount of fur, feathers or sand). Individual ID nested within zoo were included as random effects again. The results are shown in table 6.2. Once again, group size was shown to correlate with the logarithm of fGC, but none of the other factors had a significant effect (see figure 6.1).

Table 6.2: General Linear Mixed Model of group-level factors affecting the level of glucocorticoid metabolites in meerkat faeces. This analysis was based on a data set of 140 faecal samples from meerkats in 10 social groups. The minimal adequate model, excluding random effects, explained 23.1% of the variation.

Full Model	**Chi squared**	**d.f.**	**P**
Group Size	4.28	1	**0.0385**
Density	1.66	1	0.198
Condition of Sample	3.72	3	0.294
Pups Present	0.632	1	0.427
Season	0.582	1	0.446
Outdoor Space	0.151	1	0.698
Minimum adequate model	**Mean effect**	**Standard error**	
Intercept	4.22	0.444	
Group Size	-0.109	0.0481	
Random effects	**Variance**	**Standard deviation**	**Number of levels**
ID:Zoo	0.311	0.558	43
Zoo	0.438	0.662	10
Residual	0.977	0.989	

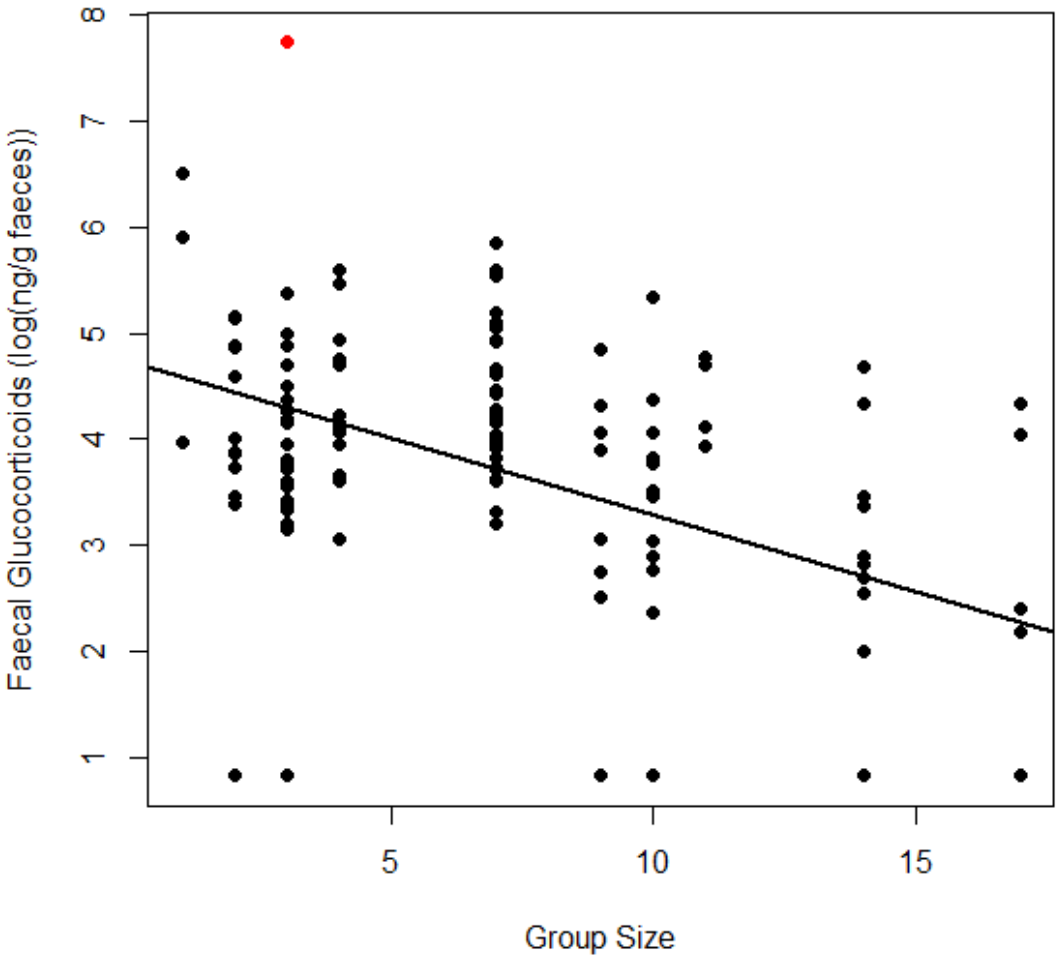

Figure 6.1: Faecal glucocorticoid metabolite levels in groups of different sizes, with line showing model prediction. Outlier is indicated in red.

If the outlier (marked in red on figure 6.1) is excluded from the analysis, it
2885 makes no qualitative difference, and group size remains significant while other factors are not (GLMM with ID nested within Zoo as random effects; group size: χ^2_1=4.03, p=0.045; outdoor space: χ^2_1=0.106, p=0.745; density: χ^2_1=1.68, p=0.196; season: χ^2_1=0.054, p=0.816; pups: χ^2_1=0.930, p=0.335; condition of sample: χ^2_1=3.79, p=0.285).

6.4.3 *Visitor effects*

The number of members of the public visiting an enclosure could have an effect either on the animals' glucocorticoid levels directly, or it could be correlated with the size of the group, and so be driving the group-size effect. For 94 of the 140 samples I had data on the number of visitors to the meerkat enclosure that day and the day before, and these were used to investigate the effect of zoo visitors on the level of faecal glucocorticoid metabolites. Six factors were tested: mean, median and maximum number of visitors observed on the day of sample collection and the same for the previous day. The results are show in table 6.3. Once again group size had a negative relationship with faecal glucocorticoid metabolites, and the number of visitor the previous day was significant: as the median visitor level increased, fGC concentrations rose; however, the maximum visitor level the previous day had a negative relationship with fGCs (see figure 6.3). Thus the lowest fGCs would be expected when there were few visitors most of the time, but a high maximum, whereas fGCs would be highest when there were a lot of visitors most of the time, but this number did not vary very much. No metric of the number of visitors on the day of collection was a significant predictor of fGC concentration, supporting the assumption that faecal glucocorticoid metabolites reflect the blood cortisol levels of the previous day.

Table 6.3: General Linear Mixed Model of individual factors affecting the level of glucocorticoid metabolites in meerkat faeces. This analysis was based on a data set of 94 faecal samples from meerkats in 10 social groups. The minimal adequate model, excluding random effects, explained 44.8% of the variation.

Full Model	**Chi squared**	**d.f.**	**P**
Group Size	13.1	1	**<0.001**
Max Visitors Yesterday	16.9	1	**<0.001**
Median Visitors Yesterday	16.7	1	**<0.001**
Max Visitors Today	1.22	1	0.269

Full Model	**Chi squared**	**d.f.**	**P**
Median Visitors Today	0.649	1	0.421
Mean Visitors Today	0.0156	1	0.901
Mean Visitors Yesterday	<0.001	1	>0.999
Minimum adequate model	**Mean effect**	**Standard error**	
Intercept	5.13	0.214	
Group Size	-0.107	0.0271	
Max Visitors Yesterday	-0.0573	0.00934	
Median Visitors Yesterday	0.209	0.0464	
Random effects	**Variance**	**Standard deviation**	**Number of levels**
ID:Zoo	0.000	0.000	25
Zoo	0.000	0.000	10
Residual	1.10	1.05	

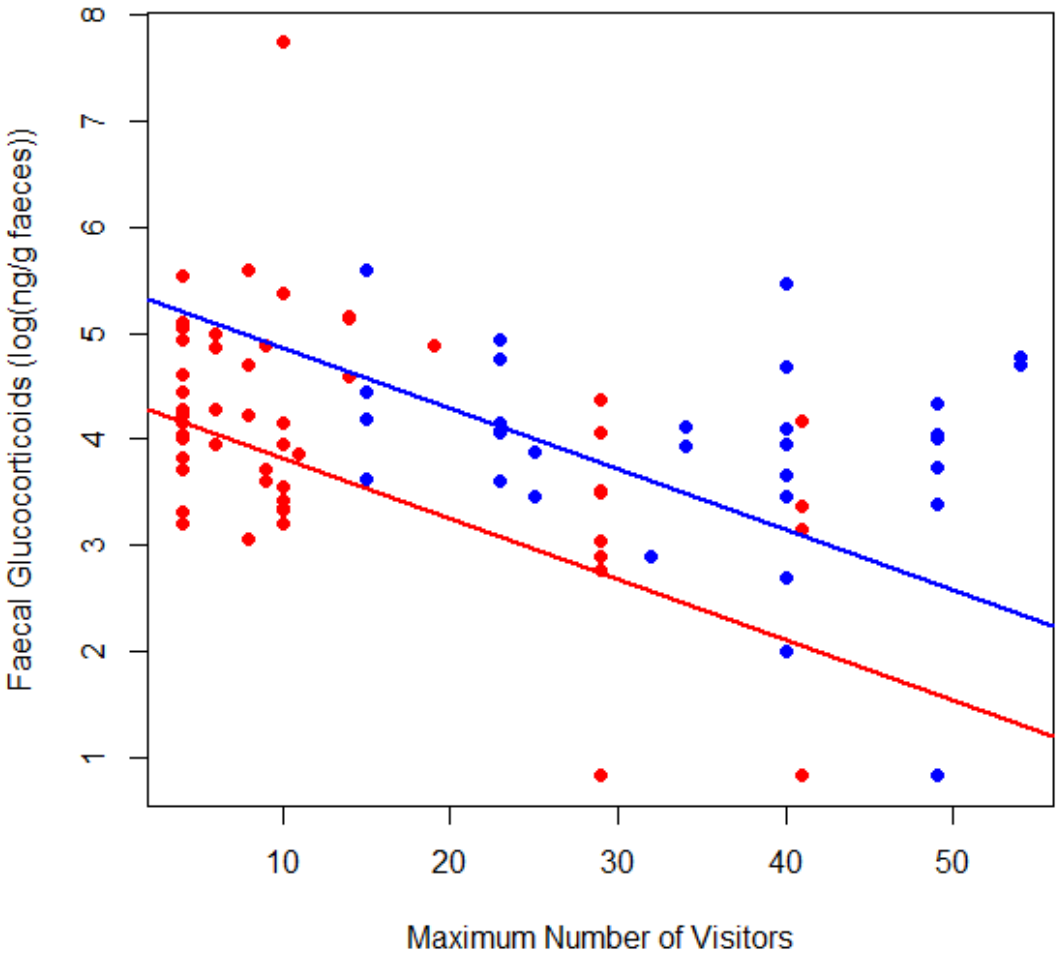

Figure 6.2: Faecal glucocorticoid metabolite levels of zoo meerkats experiencing different maximum numbers of visitors the previous day. The mean median number of visitors the previous day is 2.99 people, so this value was used to divide the data for graphical representation: samples collected the day after the median number of visitors was higher than 2.99 are marked in blue, and those when there were fewer than 2.99 visitors on average are in red. The lines show the model predictions for how fGC changes with maximum visitor number in an average-sized group, if the median number of visitors is at the first (0 visitors – red) or third (5 visitors – blue) quartile of the observed range.

6.4.4 Comparison with wild meerkats

A study on the level of faecal glucocorticoids in wild meerkats by Peter Santema (2013) using the same extraction and analysis methods found that the mean ± standard error of fGC concentration for wild males was 133 ± 98 ng/g dry mass (n=128 from 50 animals), and for wild females 132 ± 80 ng/g dry mass (n=123 from 50 animals). In the captive meerkats studied, fGC was significantly lower than that found in the wild for both sexes (males: t_{168}=3.35, p=0.001, 95% confidence intervals of differences between means from 25.3 to 97.7; females: t_{148}=4.20, p<0.001, 95% confidence intervals of differences between means from 37.6 to 104.4). However, the differences in food intake and through-put between zoo and wild meerkat mean than this comparison should be viewed with caution, as discussed below.

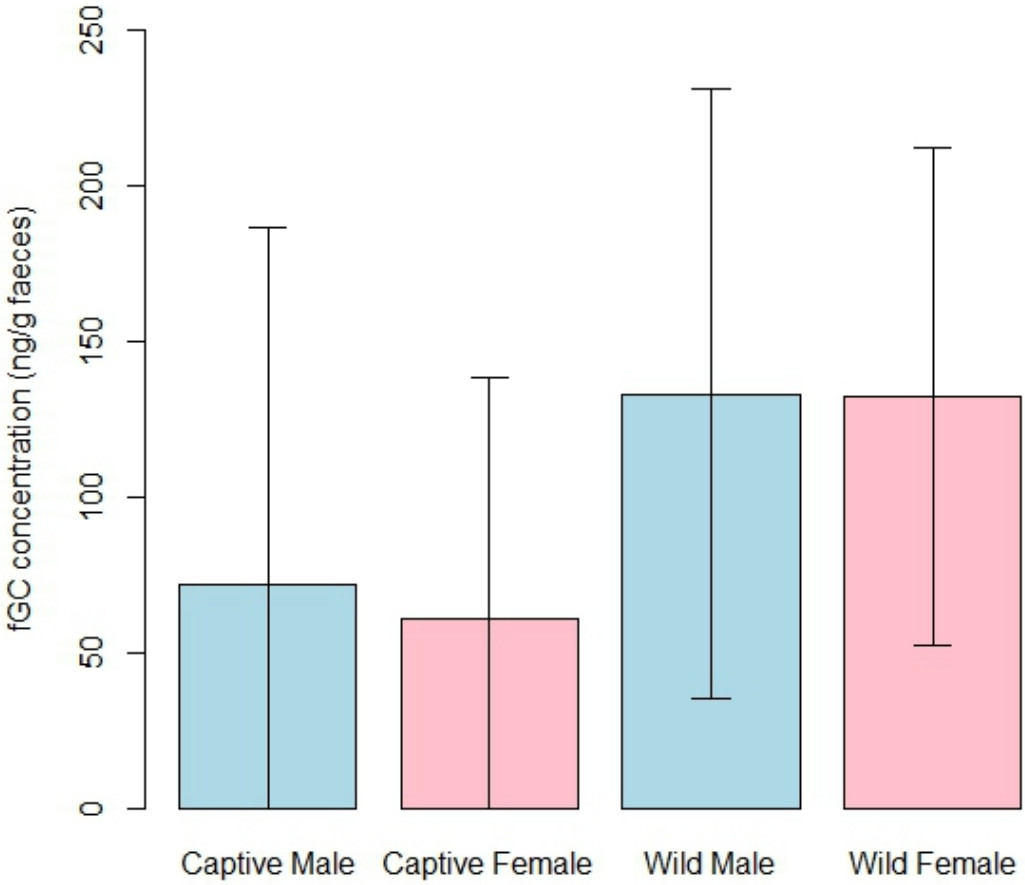

Figure 6.3: Faecal glucocorticoid metabolite levels in captive and wild meerkats for different sex categories. Bars show mean values for each category and error bars indicate standard errors.

6.5 Discussion

In this study I found that group size has a clear negative correlation with fGC. This trend is in the same direction as that found by Young (2003) who studied the faecal glucocorticoid metabolites of wild meerkats in small dispersing coalitions, but is contrary to Santema's (2013) fGC analyses in larger, stable, mixed-sex groups of wild meerkat; thus the results presented here support the

optimum group size hypothesis. I also found that the number of visitors to the meerkats' enclosure the day before the sample is collected affects hormone levels, with maximum number of visitors correlating negatively, and median number positively, with fGC. This study provides an overview of the hormonal stress experienced by meerkats in zoos, using a large number of sites to allow comparisons between different social and environmental situations.

In small splinter groups of meerkats in the wild, animals in smaller groups exhibit significantly higher fGC than those in larger groups (Young, A. J., 2003). This negative correlation of fGC with group size in smaller groups in the wild could be due to a number of factors: competition for territory, low food availability if small groups are forced into less productive areas, higher levels of contribution to cooperative activities, higher predation risk, and a trade-off between vigilance and foraging (Clutton-Brock et al., 1998; Clutton-Brock, Gaynor et al., 1999; Clutton-Brock, O'Riain et al., 1999). In captivity, many of these factors are not present, but the same pattern still emerges. It may be that, while in zoos these actual threats are not present, there is an innate hormonal stress response to being in a small group which prepares the meerkat to counter these potential risks. In captivity group size has little correlation with food provision as larger groups are fed proportionally more food, often by scatter-feeding which reduces the ability of dominant animals to monopolise a food source (Gutzmann et al, 2009); so both lower through-put and food-stress can be ruled out as causes of the group-size effect in captive meerkats (Kimble, 2003). The threat of attack from either conspecifics or predators, however, may still affect zoo animals. In wild meerkats, high blood cortisol levels have been linked to an increasing likelihood of performing sentry duty (Tatalovic, 2008). If a fear of attack is greater when in a small group, it would be expected that each animal should perform sentry duty more often, and that is what is observed (see chapter 3 for more details). This suggests that a fear of predation and/or attack from other meerkats may be a driving force in the higher fGC observed in small groups both in captivity and in the wild.

The observed effect of group size on faecal glucocorticoid concentrations could

also be explained by the effects of other factors which correlate with group size and have an independent effect on stress hormone release, but I found no support for any of the proposed mechanisms in this study. I found that none of the sex and dominance make-up of the group, the presence of pups, or the enclosure area and space per animal, had any significant effect on fGC: it appears that it is the size of the social group, rather than any coincidental factors, which affects faecal glucocorticoid levels. Amongst male meerkats in wild, it is the subordinates which perform extra-group forays which have the highest fGC levels (Young, A.J. and Monfort, 2009). Since in captivity they cannot perform these prospecting forays, it is perhaps not surprising that the expected difference between dominants and subordinates is not observed, at least in males. The lack of significant differences between subordinate and dominant females is also supported by research on wild meerkats, which showed that fGC levels between the dominance classes only differed during periods of subordinate eviction, which cannot happen in zoo populations (Young, A.J. et al., 2008). The lack of significant difference between summer and winter fGC levels is interesting, as it contradicts a previous study on the effect of season on glucocorticoids in baboons (Beehner and McCann, 2008), although rainfall and temperature have been found not to have a significant effect on fGCs in wild meerkats (Santema, 2013). Any difference in hormonal responses in the wild maybe a result of changes in environmental factors, such as food availability, rather than a reaction to the temperature *per se*.

Visitor densities did affect fGC, although the median number of visitors and the maximum number had opposite effects. The lowest fGC levels were seen in animals that had experienced a low median visitor level, but with occasional spikes of many visitors; while the highest fGC occurred when meerkats had high levels of visitors throughout the day but no large spikes in visitor number. It is not surprising that the presence of fewer people most of the time results in a lower blood cortisol level, as a stressful effect of visitors is seen in other animals (Davey, 2007; Hosey, 2000). However, this does contradict findings outlined in chapter 3, that meerkats exhibit lower levels of vigilance behaviour when there are more people present, although, as discussed there, this may be confounded

because visitor numbers are often highest at feeding times. The fact that median, rather than mean, visitor number is the significant factor suggests that the contradictory effects of maximum and average visitor number are not due to differences in the distribution of visitors. Overall, although there is a significant visitor effect, the reason for it is unclear from the results presented in this study.

Faecal glucocorticoid (fGC) concentrations appear to be lower, on average, in captive animals than in those in the wild. This may be a result of the provision of sufficient food, absence of competition for territory with conspecifics, low predation threat, and provisions to reduce environmental variation, such as heat lamps. It is not possible, however, to make clear, direct comparisons between the two using fGCs, because the concentration of glucocorticoids depends both on the amount of cortisol in the blood stream and the through-put of faeces. Due to their more regular and abundant diet, captive meerkats might be expected to exhibit lower concentrations of fGC (which are expressed as nanograms of hormone per unit dry mass of faecal matter) even if they had comparable blood cortisol levels, as a result of a change in the denominator – food intake and through-put – even if the numerator – blood cortisol – is the same. Nevertheless, the substantially lower concentrations of fGC in zoo meerkats suggest that there is not a widespread problem of chronically high blood cortisol in captivity.

From this study it is possible to highlight areas in which this technique, of non-invasive faecal sampling to assess hormonal stress in zoo animals, can be further applied: for example to remotely monitor the effects of changes in husbandry or social group composition. A prolonged elevation of blood cortisol, such as might occur in a chronically stressed animal, results over time in a blunted stress response, so that the sudden elevation in blood cortisol in response to a stressor becomes less pronounced (Busch and Haywood, 2009). Unavoidable stressful events, therefore, such as veterinary procedures or moves between zoos, provide an opportunity to assess an animal's chronic stress level by comparing baseline faecal glucocorticoids (fGC) before the event and the levels immediately afterwards. In a normal, unstressed animal a large

jump in fGC would be expected, while in a chronically stresses conspecific, which could have similar baseline values due simply to individual variation, a much lower jump would be observed due to this blunted stress response (Busch and Haywood, 2009). The technique used here could be therefore used to assess an individual animal's chronic stress, and further inform management decisions. Unfortunately, when considering fGC measurements, the normal, unstressed baseline level can vary hugely between individuals, even before variations in diet are considered. This means it is impossible to fix a general mark against which a single sample can be compared to determine if it is too high or too low, and thus fGCs cannot be used to inform management on the micro scale. In this study, however, I have used a large number of samples to demonstrate that, on a larger scale, fGCs can inform general management strategies.

Meerkats in zoos do not generally exhibit behavioural signs of stress, nor have I come across any reports of animals with health problems definitely caused by stress, but I have seen a couple of meerkats which appear to be pacing (running back and forwards along a well-worn path along the enclosure boundary) and it is not uncommon for parent-reared pups to have short, bald tails, which is attributed by keepers to over-grooming. From this study it is impossible to determine whether these anecdotal instances correlate in any way with hormonal stress.

One particularly important consequence of blood cortisol levels to cooperatively-breeding mammals such as meerkats is their effect on social behaviours. In particular, increasing levels of glucocorticoids in meerkats correlate with higher contributions to pup care (Carlson, Manser et al., 2006), although above an upper threshold the opposite effect may be observed (Ziegler, 2000) and indeed the opposite relationship is observed in the closely related banded mongoose (Sanderson et al., in prep.). In zoos it is common for meerkat pups which are not receiving sufficient care from conspecifics to be hand-reared and returned to the group after weaning; for zoos aiming to encourage parent-rearing of young meerkats, achieving this optimal level of glucocorticoid activation may be of

particular interest.

In conclusion, the levels of hormonal stress in zoo meerkats appear to be lower than in their wild counterparts, and the size of their social group and the presence of visitors appear to be the most important factors in determining this. In large groups, meerkats have a lower level of faecal glucocorticoids (fGC) than conspecifics in smaller groups. This is probably due to a higher level of perceived predation and inter-group conflict risk, as illustrated by the increased levels of vigilance by animals in small groups (see chapter 3). The age, sex and dominance status of animals are not useful predictors of fGC concentration, nor does hormonal stress alter with time of year. The number of visitors to the enclosure also has an effect on the meerkats' fGC levels, although different metrics produce different directions of effect. The results reported here suggest that the meerkats most at risk of unusually high and potentially detrimental levels of blood cortisol are those kept in small social groups, with a high median number of visitors but without spikes of high visitor numbers; therefore these groups are the ones that would benefit most from further investigation into their hormonal stress levels. From a husbandry policy viewpoint, although it is often not possible to control the levels of visitors, zoo should be aiming to keep meerkats in larger groups if they intend to minimise levels of hormonal stress.

7 Conclusion

The study of animals in zoos is important because this can inform management decisions to maximise the animals' welfare, and because zoos, at their best, can provide a naturalistic environment in which scientific research can be performed, with greater experimental control than in the wild. Multi-zoo research allows insights into how variations between zoos affect the captive animals, as well as providing an indication of how general any findings are to the captive population as a whole. Comparing zoo animals to those in the wild can inform management decisions to improve welfare, increase the success of breeding and reintroduction programmes, promote public education, and assess the relevance of zoo-based research to the broader study of that species. Social animals are a particularly interesting group to study, as the social environment of zoo animals is determined by humans, and it is important to assess the impact of management decisions on the captive animals. Meerkats are a highly social species which have been extensively studied in the wild and are commonly found in European zoos, and therefore they made an ideal study species with which to assess the impact of various aspects of the zoo environment. I studied the behaviour, endocrinology and morphology of meerkats in ten zoos in the UK and one in Germany. Several factors, including aspects of the zoo environment such as group size, enclosure size, visitor effects and climate, and behaviours such as vigilance, foraging and activity levels, came up more than once through the different areas of research. Here I bring together the conclusions from each chapter on the impact of these factors, and end with recommendations to zoo professionals which have arisen out of this research, and observations on the current systems which surround, and both advantages and limitations of, zoo-based research.

7.1 The Zoo Environment

7.1.1 Group size

The meerkats I studied were kept in groups of between one and 17 animals, with a mean group size of 7.3. In the wild group sizes are usually slightly larger, about ten to thirty animals (Clutton-Brock, Gaynor et al., 1999). In chapter 6 I found a link between group size and the concentration of faecal glucocorticoid metabolites (fGCs), a proxy for blood cortisol, high expression of which is a hormonal stress response: fGC levels were higher in those zoo meerkats kept in smaller social groups. Wild studies have found a similar negative relationship between group size and fGC concentration in small, single-sex dispersing coalitions, but a positive relationship in larger stable mixed-sex groups (Santema, 2013; Young, A.J., 2003). The zoo data supports the hypothesis that there is an optimum group size which minimises fGC levels, and hormonal stress would be higher in very small and very large groups. As the range of group sizes seen in zoos tends to be smaller than in the wild, these results suggest that zoos wishing to minimise their meerkats' fGC levels would aim for group sizes at the larger end of the range.

The size of zoo groups was not found to affect how wild-like the animals' behavioural time budgets were, but in larger groups each animal spent less time on sentry duty; the total amount of time when a sentry was present did not change with group size, so in smaller groups each individual took on a larger proportion of this cooperative behaviour. Group size was not found to correlate with enclosure size in zoos, so the density of meerkats varied between groups.

The effect of the group composition would be an interesting area for future work, but, since the social groups I studied varied so widely, from single-sex bachelor groups, to non-breeding groups of relatives, to breeding groups with various different combinations of ages and relatedness, it would be necessary

to have a larger sample of zoo groups than I was able to use. In such a social species, though, group composition no doubt plays a role in the experiences of the animals and understanding this more fully would be very informative for zoo professionals.

7.1.2 Enclosure size

I had information on enclosure sizes for 12 of the zoo groups which were studied, and the outdoor area varied from 38m^2 to 480m^2, with a mean of 157m^2. Indoor areas ranged from 1m^2 to 36m^2, with a mean of 11.8m^2. The size of the enclosure was not found to influence how wild-like its occupants' behaviour was, nor did it have any effect on fGC levels. Meerkats in large enclosures, however, were heavier than those in small enclosures; the reason for this was unclear, and further research would be needed before this could be used to inform enclosure designs. There is no support for the smaller enclosures within this range having an adverse effect on their occupants, either by altering their behaviour or causing a hormonal stress response.

7.1.3 Zoo visitors

The number of visitors to the meerkat enclosures which I studied ranged hugely: it was not unusual for whole sessions to pass without any visitors, while at the other end of the scale the entire accessible perimeter could be occupied, for example when a school group arrived or if the keepers were giving a talk. Visitor numbers were influence by weather, time of day, day of the week and time of year, but also fluctuated without obvious cause. In chapter 3 I reported that meerkats spent less time vigilant when there were more visitors present: this could be partly because high numbers of visitors were typically present at feeding times, but it is also possible that meerkats perceive the risk of predation to be lower in the presence of more humans.

High visitor numbers were also linked to fGC levels, although in a complicated and somewhat contradictory way. Levels of fGCs were lowest when there was a low median number of visitors, but a high maximum number; this is the sort of pattern that might be experienced on a weekday during school time, when there are few independent visitors in the zoo but one or two school groups. The highest fGCs occurred with high median visitor numbers but low peaks, such as might be expected during weekends or holidays, and when there are no specific attractions such as talks or feeds to attract a large number of people at one time. The presence of large median numbers of visitors being linked to a higher cortisol response is intuitive, although it does not tie in with the finding that vigilance is lower when many people are present; it is, however, difficult to account for the negative relationship between maximum visitor number and fGC concentration. This would be an interesting area for further research, especially if the number of visitors could be controlled experimentally.

7.1.4 Climate and weather

Meerkats are a desert-adapted species, but are widely kept in zoos in temperate areas. The research presented in chapter 4 showed that zoo meerkats used the sheltered part of their enclosure more often in the winter and when it was raining; the amount of time spent on social behaviour outside was much lower during the winter, but this was compensated for by the social interactions which occurred inside the house or den. The levels of fGC were not found to be significantly different in winter to in summer. Zoo meerkats' weights were show to be related to climate, with animals in zoos in warmer locations with higher rainfall generally being heavier than those in cooler, drier regions, possibly as a result of the higher amounts of energy required by the latter for thermoregulation. It is not possible to change the climate and weather experienced in a zoo, but the provision of indoor areas with heating allows the expression of important social behaviours throughout the year, and there was no support in this study for an increased level of hormonal stress in temperate areas with a cold, wet winter.

7.2 Behaviours

7.2.1 Vigilance

Vigilance behaviour is an important adaptation in a prey species such as the meerkat, and they continue to exhibit this behaviour in captivity, where predation risk is much lower than in the wild. A sentry was present for a higher proportion of time in the captive groups than is typical in the wild (Clutton-Brock, O'Riain et al., 1999), supporting the theory that sentry duty is a state-dependent behaviour mediated by hunger: since meerkats in captivity are well fed and need to spend less time foraging to achieve the same energy intake, they can spend more time on vigilance behaviour. Contribution to sentry duty was not predicted by weights, but this is also true of adult meerkats in the wild, where it is the daily weight gain rather than the absolute weight which correlates with sentry behaviour. Surprisingly, older females in zoos are more likely to perform sentry duty than younger ones; the opposite trend is seen in the wild (Clutton-Brock, O'Riain et al., 1999). The study on the effects of climate on zoo meerkats' behaviour showed that the vigilance posture is also used for thermoregulation.

7.2.2 Feeding, nutrition and activity levels

Foraging is the most common behaviour for meerkats both in zoos and in the wild, although meerkats in zoos spend significantly less time foraging during the winter, which indicates that the amount of time spent on foraging is not driven by food availability, which is the same all year round in captivity. This also means that seasonal differences in other behaviours in captivity are not driven by varying food availability, which is often identified in studies of wild meerkats as the possible driving factor (Doolan and Macdonald, 1997, 1999; MacLeod et al., 2013). With a constant year-round food supply, zoo meerkats are much heavier than wild ones. Surprisingly, however, they also spent a larger

proportion of their time active than wild meerkats. Although the activity level of zoo meerkats varies, this is not a predictor of weight. There are several potential explanations for the higher weights seen in zoo meerkats, including the possibility that the zoo population is genetically distinct from that found in the Kalahari; but based on anecdotal evidence from zoo veterinarians I understand that it is not uncommon for a build-up of fat around meerkats' internal organs to be found when post-mortems are carried out. The health and fitness consequences of these higher-than-expected weights are not yet clear, but since three quarters of zoo meerkats are obese when compared to their wild conspecifics, this should be a matter of concern to zoos keeping meerkats and a priority for further veterinary research. It would also be of great value if the feeding regimes of captive meerkats could be monitored and recorded more closely, in order to facilitate a more detailed study into the effects of diet on the health, and specifically the weight, of these animals.

7.3 Recommendations

The following observations and recommendations arising from my research may be of interest to zoo professionals wishing to inform future husbandry decisions for meerkats in their care:

- The size of enclosures and provision of heated indoor space in the zoos which I visited seem to be adequate, with no evidence from the behavioural or endocrinological data that the smaller enclosures have any negative impacts on the animals.

- The levels of faecal glucocorticoid metabolites (fGCs), a measure of hormonal stress response, are highest in meerkats in small groups. Although aggressive interactions are, anecdotally, more common in large groups, the fGC concentrations indicate that cortisol production is lower in meerkats in these groups. In the wild, small groups are more vulnerable to predation (Clutton-Brock, Gaynor et al., 1999). I would

therefore recommend that zoos attempt to keep large groups together as far as possible to minimise the hormonal stress of small group sizes.

- Meerkats in zoos are generally much heavier than those in the wild, despite spending more of their time active. Although wild weights may not be the optimum for which to aim, this divergence suggests that most zoo meerkats are being overfed. The health consequences of excess weight in meerkats are not clear, but this should be an important area of study for zoo veterinarians, and keeping a regular record of the weights of their meerkats can help zoo staff to optimise their animals' health.

7.4 Observations on zoo-based research

In general I have been very fortunate during this project to encounter many zoo professionals who are supportive of and enthusiastic about external researchers collecting data from their animals. The BIAZA research support letter is an extremely useful tool for multi-zoo researchers, providing in theory a single point of contact for assessing the value of a project and to recommend its merits to a large range of institutions; however, in reality almost all zoos also require extensive paperwork, much of which replicates the BIAZA application and is likely to deter potential researchers from extending their interest beyond a small number of institutions. A more coherent strategy between BIAZA institutions would facilitate and encourage more multi-zoo projects, and allow researchers to maximise their sample sizes. An additional advantage of a more centralised approach to research would be that new or unusual techniques, such as the glitter-feeding I used to identify faecal samples, could be vetted once by knowledgeable individuals, rather than requiring research coordinators in each institution to decide whether they thought it suitable. In all but the largest zoos there is no full-time head of research, so greater reliance on the recommendation of the BIAZA research committee would reduce some of the additional pressure placed on research coordinators by an external project.

There are forms of data which it was not possible to collect in this project but which would have provided additional insights into the effects of captivity on meerkats; mostly the constraints were due to zoo guidelines, which are enacted to ensure the safety of animals, zoo professionals, researchers and the public, and as such are completely justified. Zoos do not tend to have a Home Office licence to undertake invasive procedures, and so the extraction of blood samples without an immediate veterinary need or the restraining of an animal which causes distress, purely for research, is not possible (Hosey et al., 2009, p. 73; Smith, 2004; The North of England Zoological Society, 2011; Whitley Wildlife Trust, n.d.). In addition, I found that non-invasive activities which required contact with the meerkats, such as hair-dye marking, weighing and feeding food with glitter on it, were more difficult to carry out in zoos than with well-habituated wild mongoose groups. Meerkats in zoos, despite having regular contact with humans, are generally not encouraged to habituate to prevent them interacting too much with visitors: for example, begging for food. This does make research more difficult, but is justified since it encourages naturalistic behaviour.

Although there are huge variations in the amount and types of data kept by zoos, I have found in general that they are very generous in allowing researchers access to it. Inevitably, many of the zoos I approached to collect data in person turned the request down, and, more frustratingly, a number failed to respond to my enquiries. However, all of the zoos I did visit were welcoming and the keepers I have had interactions with have, without exception, been helpful and supportive.

In return for the support of the institutions they visit, it is the duty of researchers to provide feedback on the data they collected during their visit. Many zoos request a written report as part of the research conditions, but for maximum impact it is important that this report, or a summary of it, is seen by the keepers directly responsible for the animal in question. In addition, researchers should make their findings available more widely by publishing in peer-reviewed journals; zoo-based research is under-represented in the scientific literature,

which means that the value of zoos as research facilities is underestimated by the zoological community as a whole (Hosey et al., 2009, pp. 526–527; Pankhurst et al., 2008). As I hope has been illustrated in this thesis, zoo-based research can provide valuable information relevant both from a welfare perspective and pertaining to the scientific study of the species more generally. By taking advantage of the resource zoos provide, many research opportunities become available, which in turn can feed back into optimising the welfare of the animals under consideration, and increasing our zoological understanding as a whole.

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Appendix A – Ethogram

Following Habicher (2009 Appendix).

General behaviour

Stationary (S) incorporates:

- Lying: An animal lies on the ground in a rolled-up posture or stretched out on its back or front
- Resting: An animal sits with its lower extremities stretched forward and trunk folded forward, and with the head touching the ground in between the legs
- Low sitting: An animal sits with its lower extremities on the ground while the upper extremities touch the ground
- Low standing: An animal stands on the ground with all four extremities are on the ground

Travel (R) incorporates:

- Moving: The animal walks with moderate speed
- Running: The animal runs at a higher speed than when Moving
- Climbing: Moving vertically

Forage (F) incorporates:

- Foraging: An animal moves across the ground with ducked body and lowered tail while digging the ground superficially

- Digging for food: An animal digs in pursuit of a food item; distinguished from Dig because hindlegs are not spread
- Eating: An animal manipulates, bites or swallows a food item

Drink (Dr): Animal drinks from natural or artificial water source

Groom (G): Animal cleans its own fur with its teeth and tongue

Allogroom (A): One meerkat cleans the fur of another, either independently or reciprocally

Vigilant (V): incorporates

- High sitting: The animal sits upright, with the lower extremities and backside on the ground, while the forelimbs are bent in front of the body
- High standing: The animal stands upright with toes and footpad touching the ground, while the forelimbs are bent in front of the body

Sunbathe (Sb): Posture as Vigilant but belly is clearly directed towards the sunlight

Social Dig (Dig): The animal digs to establish or restore a burrow; its body is halfway into the burrow entrance, with the hind legs widely spread while it expels the soil between them

Huddle (H): A group of meerkats lie in close contact with each other

Playfight (P): Two or more meerkats chase, grip, push or bite one another, sometimes accompanied by vocalizations; the roles of the fighting animals change rapidly; when animals are in close contact, it is distinguished from

Huddle by the contact or attempted contact of one animal's mouth with the body of another

Keeper Interaction (K): An animal is in physical contact with some part of a human in its enclosure, or with something being held by the human

Object Interaction (EE): An animal touches or scratches a natural or artificial object for a prolonged period

Inter-specific Interaction (Int): An animal touches or directs its face and body towards an animal of a different species which is less than a metre away from it

Out of Sight (OOS)

A note on Raised Guarding

I use “Vigilance” to mean any animal high sitting or high standing, the behaviour which has been referred to in the earlier sections of this chapter, regardless of location. “Raised Guarding” is an animal in an elevated position in the enclosure that is recorded as Vigilant, Stationary or Sunbathing. There is only ever one “sentinel” or “sentry” at a time: if more than one animal is raised guarding, the session is recorded as “multiple” or “all”.

Behavioural categories not observed in captivity

Several categories of meerkat behaviour recorded in the wild were not observed during behavioural data collection in the zoos. These include: babysitting, feeding young, mobbing, fighting, frenzy and inter-group interactions.

Appendices B and C – see attached document

Appendix B – Study Locations

Zoo (social group)	Location	Group Size	Pups?[1]	Outdoor Enclosure Area (m^2)[2]	Indoor Enclosure Area (m^2)
Blackpool Zoo (pair)	53°49'N 3°01'W	2	No	202	34
Bristol Zoo	51°28'N 2°37'W	17	Yes	54	28
Chester Zoo	53°14'N 2°53'W	unknown	unknown	176	36
Cologne Zoo	50°58'N 6°59'E	unknown	unknown	480	10
Cotswold Wildlife Park (family)	51°46'N 1°39'W	10	Yes	97	4
Cotswold Wildlife Park (bachelor)	51°46'N 1°39'W	3	No	126	5
Dartmoor Zoo	50°25'N 4°00'W	2 – 4	Yes	38	2
London Zoo (ZSL Regent's Park)	51°32'N 0°09'W	unknown	unknown	unknown	unknown
Longleat Safari Park	51°11'N 2°17'W	14	No	300	0
Newquay Zoo	50°25'N 5°04'W	9 – 11	No	250	3
Paignton Zoo (family)	50°26'N 3°35'W	2 – 4	Yes	60	2
Paignton Zoo (pair)	50°26'N 3°35'W	1 – 2	No	60	2
Shaldon Wildlife Trust	50°32'N 3°30'W	6 – 7	No	50	1

[1]Were there pups under six months old at any time when I visited the zoo?
[2]Estimated from enclosure dimensions

Zoo (social group)	Marking Method	Summer Behavour Dates	Winter Behaviour Dates	Faecal Sample Collection Dates	Weights
Blackpool Zoo (pair)	visual	8/8/12-11/8/12	NA	11/8/12	No
Bristol Zoo	hair dye	19/6/12 to 22/6/12	NA	22/6/12 and 13/2/13	Yes
Chester Zoo	NA	NA	NA	NA	Yes
Cologne Zoo	NA	NA	NA	NA	Yes
Cotswold Wildlife Park (family)	spray	29/5/12 to 1/6/12	NA	1/6/12 and 12/2/13	No
Cotswold Wildlife Park (bachelor)	visual	30/5/12 to 1/6/12	NA	1/6/12	No
Dartmoor Zoo	visual	18/5/12 to 21/5/12	NA	21/5/12	Yes
London Zoo	NA	NA	NA	NA	Yes
Longleat Safari Park	hair dye	23/7/12 to 26/7/12	NA	24-26/7/12	Yes
Newquay Zoo	hair dye	4/8/11 to 12/8/11	25/1/12 to 3/2/12	4-12/8/11 and 2/3/13	Yes
Paignton Zoo (family)	visual	22/8/11 to 9/9/11	19/12/11 to 29/12/11	22/8-9/9/11 and 23/1/13	Yes
Paignton Zoo (pair)	visual	22/8/11 to 9/9/11	NA	22/8-9/9/11 and 23/1/13	No
Shaldon Wildlife Trust	hair dye	31/8/11 to 9/9/11[3]	21/2/12 to 28/2/12	31/8-9/9/11 and 17/1/13	Yes

[3]Data collected by James Bellamy as part of his BSc research project

Appendix C – Subject Animals

Data collection categories:

A: Summer Behaviour

B: Winter Behaviour

C: Faeces

D: Weight

Zoo	Enclosure	Number	Name	Transponder ID	Sex	Dominance	DoB	Birthplace	Marking	A	B	C	D
Blackpool		M03052	Jim	...0017	M	D	11/07/04	Edinburgh Zoo	Wide eyes with square mascara, small dark tail-end, longer nose	x		x	
Blackpool		M05011	Rosie	...7705	F	D	25/06/03	Blackpool Zoo	Small ears, darker muzzle, close-together round eyes, half of tail dark	x		x	
Bristol		11241	Anushka	...192	F		06/05/10	Bristol Zoo	Left shoulder and right chest	x			x
Bristol		8860	Babushka	...235	F		05/08/04	Bristol Zoo	α-feM; Right side	x		x	x
Bristol		10992	Chopin	...376	M		10/08/09	Bristol Zoo	Head	x			
Bristol		9254	Debussy	...730	M		11/07/04	Edinburgh Zoo	α-M; Right shoulder V and very dark eyes	x		x	x
Bristol		10627	Elgar	...181	M		21/02/09	Bristol Zoo	Mid back and head	x			x
Bristol		10995	Fauré	...503	M		10/08/09	Bristol Zoo	Left side	x		x	
Bristol		10737	Grieg	...796	M		07/05/09	Bristol Zoo	Base of tail	x		x	
Bristol		10738	Handel	...687	M		07/05/09	Bristol Zoo	Left thigh	x			x
Bristol		10627	Ireland	...181	M		21/02/09	Bristol Zoo	Right thigh and left chest	x			
Bristol		11243	Jenkins	...854	M		06/05/10	Bristol Zoo	Tail and left chest, pale nose; smallest adult	x			x
Bristol		12229	Liszt	...425	UNK		08/02/12	Bristol Zoo	Juvenile; Head and right foreleg	x			x
Bristol		12230	Mozart	...954	UNK		08/02/12	Bristol Zoo	Juvenile; Mid back and left jaw	x			
Bristol		12231	Newman	...583	UNK		08/02/12	Bristol Zoo	Juvenile; Base of tail	x			
Bristol			Puccini		UNK		24/04/12	Bristol Zoo	Pup; Head	x			x
Bristol			Quarantotto		UNK		24/04/12	Bristol Zoo	Pup; Left side	x			x
Bristol			Ravel		UNK		24/04/12	Bristol Zoo	Pup; Right side	x			
Bristol			Saint-Saëns		UNK		24/04/12	Bristol Zoo	Pup; Tail	x			x
Bristol		9969											x
Chester		C1068			M		22/03/10						x
Chester		C1069			M		22/03/10						x
Chester		C1076			F		22/03/10						x
Chester		C09603			M		22/02/08						x
Chester		C10194			F		05/06/10						x
Chester		C10195			F		05/06/10						x

Zoo	Enclosure	Number	Name	Transponder ID	Sex	Dominance	DoB	Birthplace	Marking	A	B	C	D
Chester		C10402			M		17/08/10						x
Chester		C10403			F		17/08/10						x
Chester		C11107			M		01/02/11						x
Chester		C11108			F		01/02/11						x
Cologne			Ace	816079	M		22/04/07		Re Hüfte				x
Cologne			Ambra	9595	F		21/04/09						x
Cologne			Ammon	5934	M		21/04/09						x
Cologne			Basti	1453	M		27/08/07		no				x
Cologne			Bela	2507	F		14/09/08		no				x
Cologne			Belinda		F		Jul-09						x
Cologne			Benji	4015	M		27/08/07		re Seite				x
Cologne			Bob	5688	M		05/02/09						x
Cologne			Bodo		M		Jul-09						x
Cologne			Bruce		M		Jul-09						x
Cologne			Cass	6076	M		22/04/07		Schwanzwurz.				x
Cologne			Eloy	674	M		27/08/07		Backe				x
Cologne			Emily	8452	F		11/04/08						x
Cologne			Farin	6277	M		14/09/08		Ohr				x
Cologne			Ferdinand	7994	M		03/02/07		Rücken				x
Cologne			Franz	84	M		03/02/07		Li Schulter				x
Cologne			Jack	4905	M		24/01/08		Mitte Schwanz				x
Cologne			Jim	7838	M		21/09/06		Kopf				x
Cologne			Lee	6325	M		27/08/07						x
Cologne			Marie	0416?	F		28/06/08		Kopf				x
Cologne			Mark	9238	M		22/04/07		Re Schulter				x
Cologne			Martie	2669	F		11/04/08		RS				x
Cologne			Meg	1751	F		24/01/08		no				x

Zoo	Enclosure	Number	Name	Transponder ID	Sex	Dominance	DoB	Birthplace	Marking	A	B	C	D
Cologne			Michael (Susi)	5338	M		03/02/07		Augenbraue				x
Cologne			Nathan	7834	M		11/04/08		dunkle Augen				x
Cologne			Per	5028?	M		28/06/08		no				x
Cologne			Percy	D3D6	M		10/10/99		no				x
Cologne			Rita	2622	F		05/02/09						x
Cologne			Rod	740	M		14/09/08		MB				x
Cologne			Stevie	886079	M		27/08/05		Nacken				x
Cologne			Whitney	9357	F		23/08/04		no				x
Cologne			Ziggy	6246	M		05/02/09						x
CWP 1	Family	1644	Chuzzlewit		F		18/03/12	CWP	Pup; medium size, mid-length tail	x		x	
CWP 1	Family	1587	Dorrit	6143	F		23/07/11	CWP	Marked right shoulder	x			
CWP 1	Family	1014	Ebenezer	2907	F		19/07/06	CWP	α-feM; heavily pregnant at start	x			
CWP 1	Family	1643	Fezziwig		M		18/03/12	CWP	Pup; largest, long tail with black tip	x			
CWP 1	Family	1465	Marley	5620	M		28/06/09	Chessington	α-M; dark 'Spock' eyes; marked mid back	x		x	
CWP 1	Family	1589	Nell	7851	F		23/07/11	CWP	No marking	x		x	
CWP 1	Family	1435	Nicholas	8456	M		22/03/10	CWP	Short tail (not offspring of α-M)	x		x	
CWP 1	Family	1588	Oliver	7164	M		23/07/11	CWP	Marked left hind leg	x		x	
CWP 1	Family	1645	Peggotty		M		18/03/12	CWP	Pup; smallest, short tail	x			
CWP 1	Family	1590	Philip	6836	M		23/07/11	CWP	Marked right hind leg	x			
CWP 2	Bachelor	MM1566	Balthesar		M		23/06/11	CWP	Biggest, round eyes, more black on tail	x			
CWP 2	Bachelor	MM1568	Caspar		M		23/06/11	CWP	Smallest, 'Strauss' eyes, lots of black on tail	x		x	
CWP 2	Bachelor	MM1567	Melchior		M		23/06/11	CWP	Bigger, narrow eyes, least black on tail	x			
Dartmoor			Makalele		UNK		17/12/12	Dartmoor Zoo					x
Dartmoor			Saffa		UNK		17/12/12	Dartmoor Zoo					
Dartmoor			Sue		F		01/01/06	Newquay Zoo		x		x	
Dartmoor			Timon		M		21/05/08	Shaldon		x		x	x
Dartmoor			Xena		F		~15/7/10	Shaldon					x

Zoo	Enclosure	Number	Name	Transponder ID	Sex	Dominance	DoB	Birthplace	Marking	A	B	C	D
Longleat	2	MK906											x
Longleat	2	MK781											x
Longleat	Main	MK715	Angola	...4820	M		13/03/03	Paignton Zoo	α-M; Weak back legs, line on tail	x			x
Longleat	Main	MK924	Botswana	...2861	M		08/05/10	Longleat	Base of tail	x			x
Longleat	Main	MK720	Cape	...0094	F		02/03/04	Blackpool Zoo	α-feM; Mid back	x		x	x
Longleat	Main	MK718	Durban	...3858	F		25/06/07	Longleat	Both shoulders	x			x
Longleat	Main	MK721	Elizabeth	...3263	F		25/06/07	Longleat	Nape of neck	x		x	x
Longleat	Main	MK074	Free.State	...3225	M		02/04/11	Longleat	Left shoulder, shorter tail	x		x	x
Longleat	Main	MK926	Gabarone	...1658	F		08/05/10	Longleat	Right shoulder, weak legs	x			x
Longleat	Main	MK071	Harare	...1805	M		02/04/11	Longleat	Both sides	x			x
Longleat	Main	MK073	Inyanga	...1731	F		02/04/11	Longleat	Left side, back and nape of neck	x		x	x
Longleat	Main	MK075	Johannesburg	...3237	M		02/04/11	Longleat	Left thigh	x		x	x
Longleat	Main	MK925	KwaZulu Natal	...2981	F		08/05/10	Longleat	Tail	x			x
Longleat	Main	MK076	Lesotho	...2832	F		02/04/11	Longleat	Stumpy tail	x		x	x
Longleat	Main	MK072	Mozambique	...1890	M		02/04/11	Longleat	Bare patch on left shoulder	x			x
Longleat	Main	MK729	Zambia	...5177	F		21/03/09	Longleat	Right thigh	x			x
Newquay			Aleksandr		M		27/07/09	Newquay Zoo	Nape of neck	x	x		x
Newquay			Bumble		M		08/05/09	Newquay Zoo	No marking	x	x	x	
Newquay			Daisy		F		17/07/10	Newquay Zoo	Right flank	x	x		
Newquay			Fraggle		F			Newquay Zoo	Both shoulders, nape of neck	x			
Newquay			Jambo		M		02/05/10	Newquay Zoo	Middle of back, below right ear and right flank	x	x		x
Newquay			Maisy		F		17/07/10	Newquay Zoo	Left flank	x	x		
Newquay			Peanut		M		02/05/10	Newquay Zoo	Base of tail and below left ear	x	x	x	x
Newquay			Peggy		F		01/01/06		Nape of neck and base of tail	x	x		x
Newquay			Simples		F		27/07/09	Newquay Zoo	Both flanks	x	x	x	
Newquay			Taz		F		17/07/10	Newquay Zoo	Right shoulder (large blob)	x	x	x	x
Newquay			Tilly		F			Newquay Zoo	Right shoulder (comma shape)	x			

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Paignton	1	8532	Amalia		F							x	x
Paignton	1	5664	Aurora		F		08/04/04	Paignton Zoo	No marking (clear stripes, darker eyes, stripes on stomach)	x	x	x	
Paignton	1	8171	Kong		M		14/03/06	Colchester Zoo	No marking (faded stripes, less mascara)	x	x	x	x
Paignton	1	8469	Pup A		UNK		10/05/11	Paignton Zoo	No marking (unidentifiable from twin)	x	x	x	x
Paignton	1	8470	Sentry		M		10/05/11	Paignton Zoo	No marking (unidentifiable from twin)	x			
Paignton	2	8172	Limpopo		M		~15/10/06	Colchester Zoo	No marking (thinner, pointier face)	x		x	
Paignton	2	5089	Machundi		F		09/07/03	Paignton Zoo	No marking (larger, round face, closer eyes)	x			
Shaldon		637	Ann	968000005315170	F		07/04/09	Shaldon	Left flank	x	x		x
Shaldon		635	Betty	968000005408832	F		07/04/09	Shaldon	Spot on middle of back	x	x		
Shaldon		634	Cuthbert	968000005303005	M		07/04/09	Shaldon	Tail	x	x		x
Shaldon		670	Dibble	968000005306163	M		14/11/09	Shaldon	Back of neck and right flank	x	x	x	x
Shaldon		684	Grub	968000005405290	M		14/11/09	Shaldon	Base of tail	x	x	x	
Shaldon		558	Kolo	956000000261741	F		12/05/06	Drusillas	No marking (scar under left ear)	x	x	x	x
Shaldon		636	Sally	968000005413914	F		07/04/09	Shaldon	Both flanks	x	x	x	x
ZSL	AdvPC6	8743			F		15/02/11	London Zoo					x
ZSL	AdvPC6	5131			F		15/07/06	London Zoo					x
ZSL	AdvRZ1	9212			M		21/08/11	London Zoo					x
ZSL	AdvRZ1	8872			M		06/05/11	London Zoo					x
ZSL	AdvRZ1	8871			M		06/05/11	London Zoo					x
ZSL	AdvRZ1	8870			M		06/05/11	London Zoo					x
ZSL	AdvRZ1	8742			M		15/02/11	London Zoo					x
ZSL	CAS16	7305			M		18/03/09	London Zoo					x
ZSL	CAS16	7304			M		18/03/09	London Zoo					x
ZSL	CLR205	E0214			F		14/09/12	London Zoo					x
ZSL	CLR205	E0213			M		14/09/12	London Zoo					x
ZSL	CLR205	E0212			M		14/09/12	London Zoo					x
ZSL	CLR205	E0211			F		14/09/12	London Zoo					x

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ZSL	CLR205	9430			F		27/01/12	London Zoo					x
ZSL	CLR205	9208			F		10/08/11	London Zoo					x
ZSL	CLR205	9185			F		10/08/11	London Zoo					x
ZSL	CLR205	8729			M		23/01/11	London Zoo					x
ZSL	CLR205	7793			F		23/02/10	London Zoo					x
ZSL	CLR205	6596			M		28/08/05	Marwell					x
ZSL	CLR205	3848			F		01/05/05	London Zoo					x
ZSL	HD 02	8730			F		23/01/11	London Zoo					x
ZSL	HD 02	8556			F		26/08/10	London Zoo					x
ZSL	HD 02	8503			F		26/08/10	London Zoo					x
ZSL	HD 02	7991			F		23/02/10	London Zoo					x
ZSL	HD 12	9211			M		21/08/11	London Zoo					x
ZSL	HD 12	9209			M		21/08/11	London Zoo					x